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STRUCTURAL MODIFICATIONS IN  
THE HAWAIIAN GOOSE  
(NESOCHEN SANDVICENSIS)  
A STUDY IN ADAPTIVE EVOLUTION

BY  
ALDEN H. MILLER

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Fig. 1. Hawaiian geese on plantation at Keolu, Oahu district, Hawaii.

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(Contribution from the University of California Museum of Vertebrate Zoology)

INTRODUCTION

AVIAN ANATOMY has taken on a dynamic character in the past ten years in keeping with similar developments in other morphological fields. It is not enough to describe structures. They must be interpreted functionally and be related to the large body of facts pertaining to natural history. When mechanical and adaptive explanations for structure are made, comparative anatomy does more than contribute a series of likenesses and differences to the study of evolution. Evolution takes place in living animals; the rôle of physiological anatomy is to determine the meaning of the evolving structures which the animal uses daily. Serving in this manner, anatomy makes a contribution to theories concerned with the mechanism of evolution instead of restricting its interests to evolution already accomplished.

This method of approach has been applied to the anatomy of mammals by such workers as Howell (1932), Hatt (1932), and Elftman (1929). With birds, Stresemann and his associates have been most active in physiological-anatomical investigations. Previous work upon geese has been done in connection with broad surveys of adaptation within the class Aves. Stolpe's (1932) study of the hind limb, including that of geese, has been useful to me. Since he dealt chiefly with the mechanics of joints, this paper is complementary to his. Furthermore, it presents comparisons among closely related forms, which were not attempted by him.

The Hawaiian goose (*Nesochen sandvicensis*) is one of three anserine birds endemic to the Sandwich Islands. The other two are ducks, both classified in the genus *Anas* in its more inclusive sense. Neither duck has become strikingly modified in comparison with continental members of the genus. In contrast to them, the Hawaiian goose, through its peculiar foot structure, has attracted attention as a distinctly modified insular form. The trend of specialization in this species, in comparison with that in the majority of geese, is toward a non-aquatic running and climbing habit, with restriction of flying power, and absence of migration. Among the ducks there are numerous insular forms, but few geese have become so restricted in distribution. *Nesochen* may be regarded as the most isolated of all geese; it probably has a smaller range than any other member of the group. It does not represent, however, the extreme of land-dwelling adaptation within the Anseriformes, since *Anseranas* of Australia appears to have carried this specialization still farther.

The possibilities which *Nesochen* presents for a study in adaptation should be apparent. I propose to analyze structure and movement, particularly of the hind limb, in relation to the habits of the species. The North American species used for comparison will be dealt with in similar manner. Because within the Anserinae close similarity in musculature prevails (Beddard, 1898, p. 459), the innervations of muscles such as may be determined from macroscopic dissection seem to be of slight importance for this study. Muscles are readily homologized throughout the group on the basis of position. Adaptations often are matters of proportions of parts. The hind limb embodies most of the differences associated with locomotion.

Another purpose of this study is to search out characters which will serve to establish the natural relationships of this monotypic genus, *Nesochen*, to other members of its family. The question of relationships has never been considered fully, certainly not on the basis of anatomical study.

Furthermore, it seems important to record such facts as can be learned about so unusual a species that possibly is doomed to early extinction except as human fancy continues its existence either through rigid protection or by means of captivity.

#### MATERIALS

The opportunity to study *Nesochen* has come through the interests of Miss Annie M. Alexander and Mr. Jack Waterhouse who, appreciating the values that might accrue from study of specimens in-the-flesh, have been alert to obtain, in good condition, birds that have died from natural causes. For their invaluable assistance and the coöperation of Dr. Joseph Grinnell I am indeed grateful.

Four specimens of *Nesochen sandvicensis*, all from Keau, Olaa district on the island of Hawaii, have been available. These birds had existed in a semi-wild condition on one of the large plantations of the island. (1) No. 59136 Mus. Vert. Zoöl.; ♀ died on nest, December 1, 1931; hatched in 1926; skin and complete alcoholic specimen; one wing clipped. (2) No. 60896; ♂ (*sic* Jack Waterhouse), skin and complete skeleton; died about June 1, 1932; about nine months old; body molting; wing unclipped. (3) No. 60923; ♀ received, San Francisco, July 7, 1932; skin and partial alcoholic specimen; body molting; wings unclipped; probably about one year old. (4) No. 62789; ♀ died February 1, 1933, hatched December 4, 1932; saved as skin and nearly complete alcoholic specimen; in juvenal plumage, remiges only partly grown.

Alcoholic specimens of North American genera, vital to the conduct of this work, have been procured almost entirely through the efforts of Mr. James Moffitt, to whom I am greatly indebted. One example each of *Branta canadensis minima* (♂), *Branta nigricans* (♂), *Anser albifrons albifrons* (♂), *Chen hyperborea hyperborea* (♀), and *Philacte canagica* (♀) have been dissected. Dr. Alexander Wetmore has kindly loaned skeletons of *Chloëphaga* from the collection of the United States National Museum and Dr. Hildegarde Howard has placed all the goose skeletons at the Los Angeles Museum at my disposal.

## NATURAL HISTORY OF THE HAWAIIAN GOOSE

In order to interpret the structural modifications of *Nesochen* in the light of its habits, it is necessary to summarize here facts pertaining to the natural history of the species.

*Distribution.*—The species is now limited to the island of Hawaii, comprising an area of 4015 square miles, but it is reported to have bred on the adjacent island of Maui in past times (Perkins, 1903, p. 457).

*Habitat.*—On Hawaii the geese occupy two regions, one above the dense humid forest belt, the other below. Both areas apparently represent the extreme of barren, arid areas upon the island. Henshaw states that above 5000 feet, "the range of this goose is quite extensive, and it is found from the district of Kona to the northeast flanks of Mauna Kea. . . . The region it affects is open, and, in general, as barren as can well be imagined, consisting for the most part of lava flows, naked except for very scanty growth of ferns, ohelos, pankeawe, and a few other lowly shrubs. Except for the temporary rain-water pools this region is entirely devoid of water, and it is doubtful if this goose drinks, or indeed cares to drink, any other fluid than the dew it may find on the grasses and berries it eats. The bird has lived so long amid its novel surroundings that it . . . never enters water, but is in all essential respects a land goose."

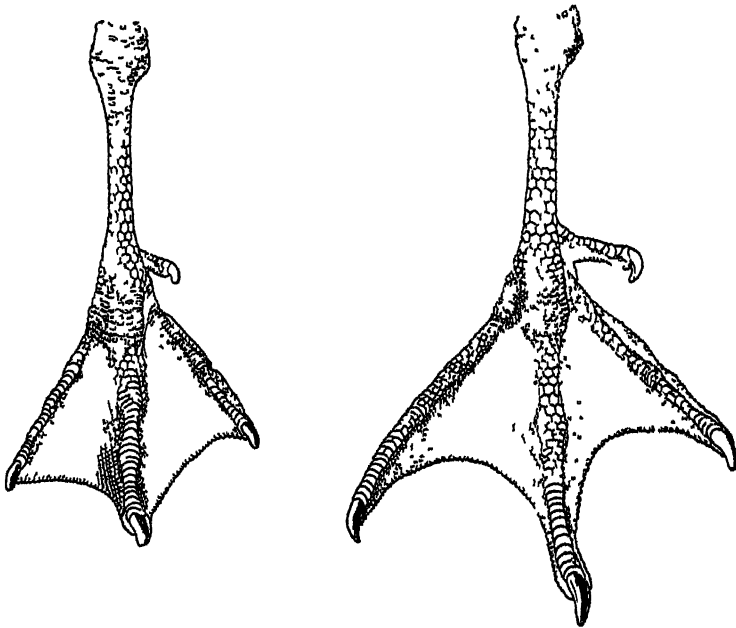
The lowland habitat is principally below 1200 feet elevation where the geese frequent barren lava flats near the sea in the districts of Puna, Kona, Kau, and Kahala. On these flats, there is evidently a considerable amount of green food, despite their barren appearance. Henshaw describes this region as a winter and breeding habitat. He is not clear concerning the precise part of the year in which the birds occur in the lowlands but states that they leave the uplands in early fall, apparently returning, I infer, some time in the early spring. The greater number, probably all, leave the "upper grounds." Thus, it is not certain how uniform or how extensive is this seasonal shift.

*Migration.*—A true migration is certainly lacking. Even the supposed straying to other islands of the group is discredited on the grounds of misidentification of the birds in question. The migratory North American species which reach the islands in small numbers in winter have not been reported in company with *Nesochen*. These North American migrants are now known to include: *Branta nigricans*, *Branta canadensis minima*, *Oen hyperborea hyperborea*, *Anser albifrons*, and *Philaule canagica*. The seasonal movements as described by Henshaw are not known to involve any extensive flights; in fact the movement may be accomplished in part on foot or by means of short flights such as would be regularly employed in moving about over the feeding grounds.

*Foraging.*—Hawaiian geese feed upon tender grasses, weeds, and berries. Henshaw emphasizes the pualele (*Sonchus oleraceus*), a milky-juiced weed, as the principal food; various berries also are eaten. One may surmise that the birds browse in the scrubby plant growth covering the irregular terrain of



their habitat. In comparison with winter flocks of geese in North America there is probably less feeding on short grass and on grain growing on open level surfaces and there appears to be no foraging in the mud at the edges of ponds and marshes. On the average, the food used by *Nesochen* would seem to be of a softer nature despite the nonaquatic proclivities of the species.



*Branta nigricans*

*Nesochen sandvicensis*

Fig. 2. Feet of *Branta nigricans* and *Nesochen sandvicensis*,  $\times \frac{1}{2}$ . Note reduction of web and large nails and hallux in *Nesochen*.

*Progress on land.*—Rothschild writes (1900, p. 281): "... the legs and feet are altogether very strong and large, causing the birds to stand and walk very firmly and very high. . . ." A similar impression was gained as I watched a captive Hawaiian goose at the zoölogical gardens in Washington, D. C. Not only did the bird stand high and well balanced but the ease with which it walked and ran suggested a great reserve of cursorial power. Contrasted with species of *Branta* the legs seemed to swing more freely and the body lacked motion from side to side. In the recovery stroke, the tarsus was raised especially high and thrust forward with the long toes only slightly flexed, the position resembling that assumed by a pheasant. The flexibility of the toes, freed by the reduction of the web, was evident as the feet adjusted themselves to the slight irregularities of the ground (see fig. 2). This captive bird was decidedly restless, pacing back and forth, rather than standing stolidly as do many captive geese.

One may readily envisage this instinctive gait put to good use in the rough, sometimes steeply inclined, lava beds as the bird climbs, jumps, and runs through broken rock, brush, and grass tussocks.

*Swimming.*—*Nesochen* does not resort to water for protection, even when in a flightless condition. The consensus is that the geese never visit the ponds of the lowlands or the seashore. Perkins states (*op. cit.*, p. 458): "In many of its upland haunts it certainly seems to avoid the wetter and more marshy localities. In captivity however, it sometimes acquires a very decided liking for water and will enter readily enough." That it can swim is evident, but the proficiency of the act is not known to me. It should be emphasized, however, that normally swimming is never an avenue of escape nor is it an agency in foraging. Apparently *Nesochen* is the only anserine whose young are not reared in part on the water. Its habitat preferences definitely keep it away from bodies of standing water. Ability to swim would seem to have no utilitarian value in this species.

*Flight.*—No mention is made of any noticeable weakness of flight. Peale (1848, p. 249) speaks of its powers of flight as being sufficient to enable it to move to as great distances as does any other member of the genus (*Branta* or *Bernicla*). Cassin (1858, p. 339) however writes: "Dr. Pickering, in his journal, . . . states that . . . when disturbed, [it] flies off, near the surface of the ground, without rising in the air, like the species of North America." This suggests to me the flight of *Branta nigricans* which, with that of *Philacte canagica*, is conceded to be more labored than that of other species of *Branta* not maritime in habit. It is perhaps significant that no one has described *Nesochen* rising into the air and circling about over its feeding grounds. Flight, then, is less frequently and extensively indulged in by this insular form than by its continental relatives.

*Molting.*—There is not a gradual replacement of remiges in adaptation to terrestrial habitat as there is with *Anseranas* (Heinroth, 1931). The Hawaiian geese undergo the annual flapper stage customary in geese. Henshaw (*loc. cit.*, p. 106) remarks: ". . . when leading about their young . . . the old birds undergo the moult, and, when deprived of their wing feathers and unable to fly, they, and the young, are easily run down by the fleet-footed natives." This shows that they molt in January and February following the breeding season, as is normal.

It must be made clear that the four available specimens of *Nesochen* were not birds taken in the wild and so did not experience as individuals all the conditions of existence outlined above. They all existed in a semiwild condition on one of the large plantations of Hawaii. The ground, though irregular to a moderate degree (fig. 1), was not the usual lava-barren habitat, and a pond was available to them. The birds were allowed to feed at large and were noted by Mr. Waterhouse flying over fences at will. The adult female, however, was wing-clipped, but the development of the pectoral muscles seems to indicate that she had flown at one time. The two immatures had normal wings. The musculature of the wings of the juvenile is not fully developed; the muscles of the hind limb are well formed. The condition of its pectorals stands in pronounced contrast to that of the other two samples. The life of the four specimens, although subject to certain abnormalities of environment, in many

respects permitted normal *Nesochen* behavior. The conditions were not so severely abnormal, aside from the wing clipping of one bird, that they should have seriously interfered with the manifestation of hereditary structural adaptations of the species to its normal environment.

#### SUMMARY OF THE NATURAL HISTORY OF SPECIES USED FOR COMPARISON

*Philacte canagica*.—Breeds in Alaska from north of Cape Prince of Wales, south to mouth of Kuskokwin River and on St. Lawrence Island. Migration not extensive, although occasional individuals stray south to California. Winters in southern Alaska, but chiefly along shores of Aleutian Islands. Breeding habitat, flat marshy islands bordering sea. Forages on breeding grounds on mud flats and tundra near sea, procuring chiefly shellfish and some berries. Winter habitat in California, inland marshes. Next to sea brants, probably most maritime of geese; hind limbs used not so exclusively for swimming as they are in *Branta nigricans*. Flight resembles that of *Branta nigricans*, but *Philacte canagica* not as agile on the wing.

*Branta nigricans*.—Breeds on Arctic coast and islands from Point Barrow east to near mouth of Anderson River. Migrates to Pacific coast, wintering on salt water from British Columbia to Lower California. Breeding habitat, small islets in fresh-water ponds (near seacoast) and along marine shore line and offshore islands. Forages (at least in winter) entirely in water, eating chiefly eel grass. Roosts at times on rocks along shore and on sand bars; not known to walk any appreciable distance under normal conditions. Excellent swimmer; feet used almost exclusively for this act. Flight by short energetic wing strokes as in heavy-bodied, short-winged ducks; does not rise high above water or ground but maneuvers in flock formation over feeding area and along shore line.

*Branta canadensis minima*.—Breeds in Alaska, on Aleutian Islands, and along coast of Bering Sea. Migrates, wintering from British Columbia to southern California. Breeding habitat, chiefly in interior, extending from seashore far inland along large rivers, frequenting grassy borders of ponds and sand bars. In winter, inhabits interior marshy lands. Forages (in California) on open alluvial plains of valleys, grazing on short grass and on occasion eating grain, which activities involve extensive walking and some running. Resorts to water, often tule marshes, at night and in midday, where it spends considerable time swimming. Flight strong with powerful sweeping wing strokes. Flies a great deal in going to and from feeding grounds and in flock maneuvers over winter habitat. Flight usually well above surface of ground; is able to rise abruptly from ground, so differing from foregoing species. Despite relative greater length of tarsus compared with that of other races of *Branta canadensis* (see Grinnell, Bryant, and Storer, 1918) information about habits fails to indicate greater walking proclivities in this race, although it appears to walk with greater ease (see p. 22).

*Anser albifrons albifrons*.—North America and eastern Asia; in North America breeds on Bering Sea and Arctic coasts. Migrates, wintering chiefly west of Rocky Mountains and south of Canadian line. Breeds in grassy or sandy places in flat terrain close to water.

*Chen hyperborea hyperborea*.—Breeds only on Arctic coast from Mackenzie River to Hudson Bay. Migrates, wintering chiefly south of Canada in the United States. Breeding habitat, flat barren lands or marshy ground, as along shore of Southampton Island, Hudson Bay. This form and the two preceding, on basis of available information, cannot be differentiated significantly with regard to habitat and general activity during the winter period.

In summary, the comparative material consists of species, primarily North American, breeding in far northern latitudes, and, except for *Philacte*, migrating extensively. All species frequent water or marshy places and swim readily; apparently all can dive if necessary. *Branta nigricans* spends the greater part of its time in salt water. *Philacte* is less closely attached to the water, but is more maritime than the other three species. *Branta canadensis minima* is perhaps the most given to wandering on land. None is truly an upland goose living on steep or rugged terrain.

## MUSCLES OF THE HIND LIMB

The muscular anatomy of geese has been most completely dealt with by Fürbringer (1888). His work on the fore limb of *Anser cinereus* makes it unnecessary to repeat detailed accounts of the wing muscles. There remains to be described the musculature of the hind limb as a basis for detailed comparisons among members of the Anserinae. These accounts are based on a dissection of the hind limbs of three specimens of *Nesochen*: a nearly full-grown, actively running gosling; a yearling; and a six-year-old breeding bird, heavily muscled throughout. The different ages of these specimens afford opportunity to set aside features which are the result of age and to emphasize the true, assumedly inherent, characteristics of the genus. Each account applies equally well to *Branta c. minima*, *Branta nigricans*, *Philacte canagica*, *Chen hyperborea hyperborea*, and *Anser albifrons albifrons* except as specified in the comparative statements that frequently are included.

Total weights are here listed so that the reader may evaluate the comparative measurements of origins and insertions in relation to the size of the bird.

|                                           |           |
|-------------------------------------------|-----------|
| <i>Nesochen sandvicensis</i> no. 1.....   | 1847.5 g. |
| <i>Nesochen sandvicensis</i> no. 4.....   | 1236.0 g. |
| (hind limbs not proportionately so small) |           |
| <i>Branta c. minima</i> .....             | 1600.0 g. |
| <i>Branta nigricans</i> .....             | 1600.0 g. |
| <i>Philacte canagica</i> .....            | 1417.5 g. |
| <i>Anser albifrons albifrons</i> .....    | 2170.0 g. |
| <i>Chen hyperborea hyperborea</i> .....   | 1846.0 g. |

Apart from a consideration of these weights, it should be borne in mind that the linear measurements of the skeletal parts of the hind limb of *Nesochen* are

as great as those of *Anser albifrons*. The weight of specimen no. 3 of *Nesochen* was not procured.

Muscles are listed in a sequence most easily followed in a progressive dissection of the limb. As a matter of convenience, the terminology follows that of Burt (1930) and this in turn corresponds closely with that of Shufeldt (1890). The terminology of these authors frequently does not indicate homology with mammalian or reptilian muscles. The determination of such homology is not the function of this study; there has been no attempt to remedy some of the illogical terms in Shufeldt's system.

While this paper has been in press, Hudson's (1937) comparative survey of the musculature of the pelvic appendage in various orders of birds has appeared with a combination of Gadow's nomenclature (1891) and the B N A nomenclature. He follows closely Gadow's opinions on homology with mammalian muscles. The majority of the names used by me may be traced in Hudson's synonymy through the listing of Shufeldt's names. Where Shufeldt did not supply a name, I have used Gadow's name.

#### M. SARTORIUS

Broad, flat muscle occupying anterior margin and part of anteromedial surface of thigh (figs. 3 and 4).

*Origin*.—Fascia from vertebral border of ilium and entire neural spine of last free lumbar vertebra. In *Branta* and *Anser* extends anteriorly only to margin of last free vertebra; in *Chen* extends to middle of last free vertebra; *Phalacrocorax* similar to *Nesochen*. Width of origin, 27–28 mm.; *Phalacrocorax*, *Chen*, and *Anser*, 22–23 mm.; *Branta nigricans* and *Branta c. minima*, 15 and 19 mm., respectively.

*Insertion*.—Partly fleshy on medial and anterior surface of patella and on adjacent inner cnemial crest of tibiotarsus. Width just proximal to insertion, 11–13 mm. in all except *Branta nigricans* in which it is 6.5 mm.

#### M. GLUTEUS PRIMUS

Broad, and extremely thin muscle on lateral surface of thigh just caudal to M. sartorius (fig. 3).

*Origin*.—Fascia on iliac crest beginning adjacent to that of M. sartorius and extending posteriorly 35 mm.; 47–48 mm. in *Chen*, *Anser*, and *Phalacrocorax*. Line of junction of muscular tissue with fascia of origin nearly straight in *Nesochen*, but more or less curved dorsally at anterior end in other forms, especially in *Branta nigricans*.

*Insertion*.—Fascia that joins sheath of M. extensor femoris beneath and runs with it to become strong tendon attaching to tip of outer cnemial crest and to patella. Distal contour of muscular tissue strongly convex dorsally so as to produce two fleshy tongues directed ventrally, separated by central fascia. Central fascia more extensive in *Nesochen* than in other forms.

#### M. GLUTEUS MEDIUS

Short thick muscle beneath M. sartorius, occupying most of concavity of ilium.

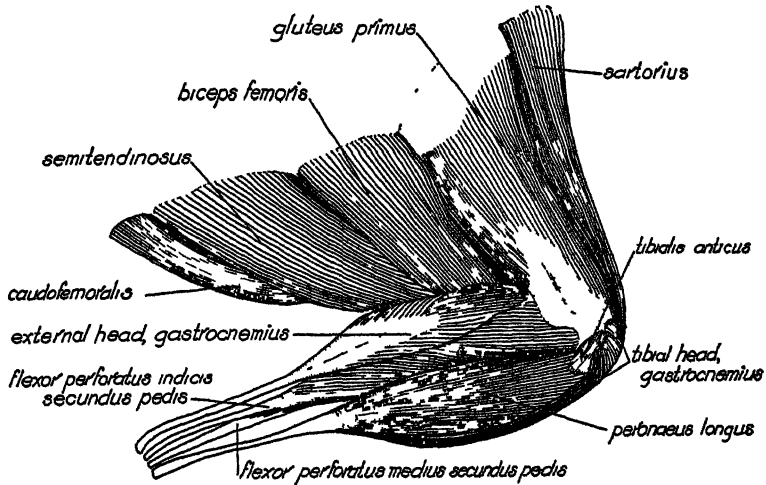
*Origin*.—Fleshy from dorsolateral surface of ilium on and below anterior iliac crest and above M. gluteus minimus. Limits of origin anteriorly and dorsally usually more rounded in *Nesochen* than in other genera (fig. 4), corresponding to shape of iliac crest which is arched and deflected downward to lesser degree in latter. Iliac depression, and hence origin, more extensive anteriorly in *Nesochen* than in other genera, *Chloephaga* excepted. *Nesochen* differs from all in more perpendicular angle of dorsolateral iliac surface.

*Insertion*.—Aponeurosis on external surface of femur just posterior to trochanteric ridge. Anterior extension of origin causes relatively larger part of muscle fibers to run horizontally to insertion in *Nesochen* than in others.

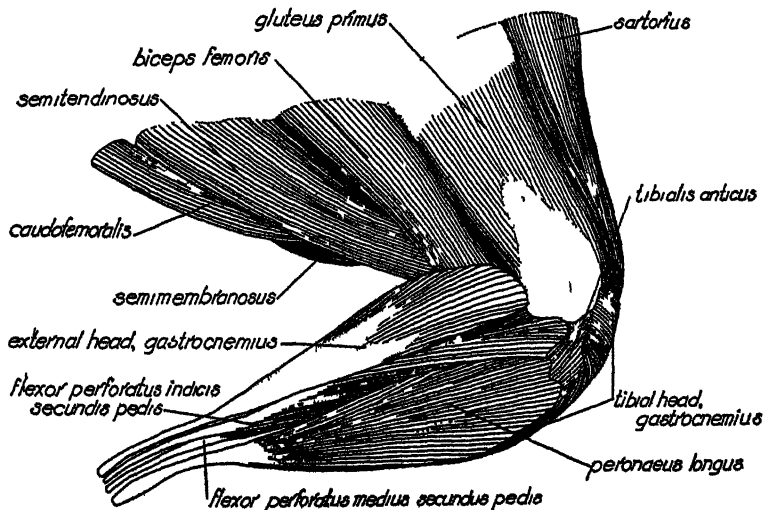
**M. GLUTEUS ANTERIOR** (of Beddard; ilio-femoralis externus of Gadow)

Small short wedge-shaped muscle lying between M. gluteus medius and M. biceps femoris.

*Origin*.—Fleshy from iliac crest above acetabulum; width about 7 mm.; proportionately greater in *Anser*.



*Branta canadensis minima*



*Nesochen sandvicensis*

Fig. 3. Comparison of superficial musculature of hind limb. Right legs of *Branta canadensis minima* and *Nesochen sandvicensis* (specimen no. 1),  $\times \frac{1}{2}$ .

*Insertion*.—Aponeurosis passing external to that of M. gluteus medius to attach well below insertion of latter on external surface of femur opposite lower part of insertion of M. obturator externus. In *Anser* and *Oen* insertion is slightly farther distad, opposite ventral margin of M. obturator externus.

**M. GLUTEUS MINIMUS**

About one-fourth size of *M. gluteus medius* beneath which it lies on ventral border of ilium.

*Origin*.—Fleshy on entire ventrolateral margin of ilium anterior to acetabulum. In *Anser* and *Phalacrocorax* attachment to border lacking for 8 mm.; *Chen* approaches condition in *Branta* in which origin not quite as extensive as in *Nesochen*.

*Insertion*.—Short aponeurosis just ventral to insertion of *M. gluteus medius* on external surface of femur.

No separate *M. gluteus quartus* identifiable, but slight tendency to subdivision of a dorsal part of aponeurosis of *M. gluteus minimus* may indicate fused *gluteus quartus*. *Phalacrocorax* alone shows distinctly divided aponeurosis and somewhat distinct group of muscle fibers representing *M. gluteus quartus*.

**M. EXTENSOR FEMORIS**

Large thick muscle covering lateral surface of femur internal to *M. gluteus primus*, varying markedly in size in different genera (fig. 4).

*Origin*.—Anterior head (cruraeus), fleshy from anterior surface of neck of femur and from trochanteric ridge; posterior head (vastus externus) fleshy from posterior outer surface of neck and trochanter of femur and tendon of insertion of *M. obturator externus*. Two heads join distal to insertion of *M. gluteus minimus*. Fibers also arise on femur from this point distally to end of shaft.

*Insertion*.—By heavy flat tendon in common with fascia of *M. gluteus primus* (p. 8).

**M. BICEPS FEMORIS**

Large moderately thick muscle lying just posterior to *M. gluteus anterior* and *M. extensor femoris*; no indication of two heads.

*Origin*.—By short fascia and fleshy attachments on posterior iliac crest, 27–33 mm. in anteroposterior extent; extent of origin in *Anser*, 40 mm.; in *Phalacrocorax*, *Anser*, and *Chen* origin overlapped by *M. gluteus primus* 3 mm. or more.

*Insertion*.—Principally by tendon running through tendinous sling attached to femur (fig. 5) to pass to tubercle on posterolateral surface of fibula slightly distal to proximal end of fibular crest; also by smaller posterior tendon to fascia of medial surface of external head of *M. gastrocnemius*. In *Chen* only, this insertion on *M. gastrocnemius* essentially lacking, perhaps being represented by weak fascia at this point. Tendinous loop from femur attached laterally to fascia and tendon of external head of *M. gastrocnemius*, running with these to external condyle of femur; medial attachment on shaft of femur just proximal to external condyle; bend of loop held in place by tendon running at a 90-degree angle to loop, and attaching to external margin of fibula just distal to head, and to ligament joining head of tibiotarsus and external condyle in common with tendons of origin of long flexors of toes. Distance of principal *M. biceps femoris* attachment from articular surface of tibiotarsus slightly less in *Nesochen* than in other forms, resulting in shorter lever arm for action of this muscle. (For further discussion of leverage, see pp. 28–30.)

**M. SEMITENDINOSUS**

Broad, shallow muscle posterior to *M. biceps femoris* on posterolateral surface of thigh.

*Origin*.—Fleshy, and by weak fascia from posterior iliac crest, beginning about 2 mm. posterior to *M. biceps femoris*; extends posteriorly along ilium to transverse processes of first two or three free caudal vertebrae. In *Phalacrocorax* and *Anser* separated at origin from biceps by 10–11 mm. space through which iliac head of *M. caudofemoralis* is visible beneath; separation in *Chen*, 7 mm.

*Insertion*.—Short weak flattened tendon in common with *M. semimembranosus* to prominence on medial surface of shaft of tibiotarsus below rim of head; point of attachment relatively more proximal in *Nesochen*.

**M. SEMIMEMBRANOSUS**

Small ribbonlike muscle medial to *M. semitendinosus*.

*Origin*.—Short weak fascia from ventral border of ischium.

*Insertion*.—See insertion of *semitendinosus*.

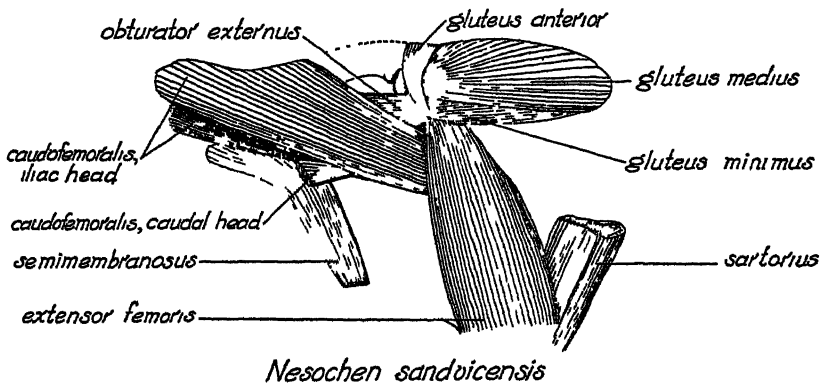
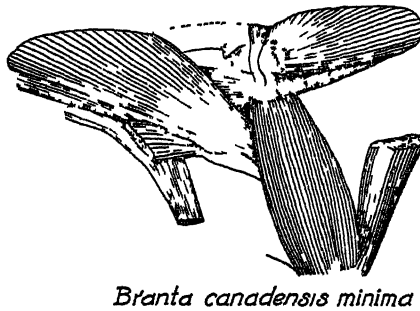
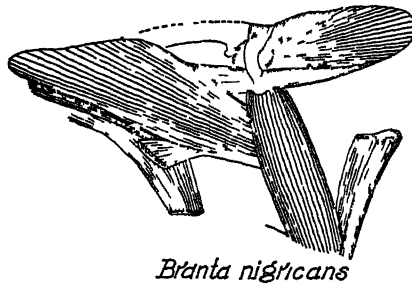


Fig. 4. Comparison of deep musculature of thigh. Right legs of *Branta nigricans*, *Branta canadensis minima*, and *Nesochen sandvicensis* (no. 1),  $\times \frac{1}{2}$ .

**M. CAUDOFEMORALIS**

Essentially two separate muscles flattened against synsacrum, medial to *M. biceps femoris* and *M. semitendinosus*; larger division has no connection with tail.

*Origin*.—Iliac head (accessory caudofemoralis), fleshy from posterior margin of ilio-ischiatic fenestra, surfaces of ilium posterior and dorsal to fenestra, extending to posterior margin of ilium, and surface of ischium posterior and ventral to ilio-ischiatic fenestra, extending ventrally to margin of *M. semimembranosus*. Posterior attachment on ilium more extensive in *Nesochen* than in other geese with fibers correspondingly more horizontal in direction in *Nesochen*. Dorsal margin of origin distinctly concave in *Nesochen* (fig. 4) and



*Philacte*, though in latter, posterior dorsal margin nearly straight or even slightly convex. Although margin might be expected to vary individually, three specimens of *Nesochen* entirely uniform.

Caudal head fleshy from ventral border of pygostyle.

*Insertion*.—Caudal head joins iliac head as tendon on ventral border of latter to become surrounded by muscle fibers of iliac head; ventral borders of iliac head thus separated into lateral and medial layers; separation visible posteriorly as far as origin; enclosed tendon of caudal head merges with tendon of iliac head close to femur to make common attachment on line 18 mm. long on posterior aspect of shaft of femur.

Caudal division relatively larger in *Branta* and ventral border of iliac head tendinous after junction of caudal division (especially in *Branta c. minima*), thus immediately forming common tendon without fleshy enclosure of caudal tendon; however, division of fibers of iliac head visible posterior to junction of tendons.

In *Philacte* caudal division relatively large as in *Branta* but junction of two divisions as in *Nesochen*.

In *Anser* caudal head relatively large and fully enclosed in fibers of iliac head; fleshy part of iliac head gives way to tendon almost immediately upon junction of caudal head, much as in *Branta*, but tendon appears across at least three-fourths of width of iliac head at this level, not merely on ventral border as in *Branta*; width of insertion on femur 23 mm.

In *Chen* junction of two heads similar to *Nesochen* with caudal head tendon fully enclosed and no tendon on ventral border of iliac head; common tendon short as in *Nesochen*, but width of insertion 23 mm.; caudal division larger throughout than in *Nesochen*; mediolateral subdivision of iliac head absent at origin and only faintly visible at point of junction of heads.

#### M. ADDUCTOR LONGUS ET M. ADDUCTOR MAGNUS

An essentially single, flat muscle lying medial to iliac head of M. caudofemoralis.

*Origin*.—Partly fleshy, partly by fascia on pubis, ventral border of ischium and fascia of entire ischio-pubic fenestra. Extent of fleshy part posterior across fenestra and on ischium somewhat variable, being especially extensive in specimen no. 1 of *Nesochen*, less so in other specimens of genus and in other geese dissected. Partial delamination anteriorly of belly into medial and lateral parts visible in three specimens of *Nesochen*; two divisions completely merged posteriorly. In all forms except *Nesochen* posterior margins of two divisions visible also.

*Insertion*.—Chiefly fleshy to crest bordering popliteal area medially, beginning just proximal to internal condyle of femur. Anterior border of muscle bound by weak fascia to entire posteromedial surface of femur.

#### M. OBTURATOR EXTERNUS

Thick narrow muscle lying over ilio-ischiatic fenestra dorsal to M. adductor longus.

*Origin*.—Fleshy on ischium and anterior part of fascia covering ilio-ischiatic fenestra.

*Insertion*.—Flat tendon, 8 mm. wide on external surface of femur opposite insertion of M. gluteus minimus; insertion relative to that of M. gluteus minimus slightly higher in *Chen* and *Anser*.

#### M. OBTURATOR INTERNUS

Bipennate muscle lying within ischio-pubic fenestra, covered laterally by fascia stretched across fenestra. Bipennate arrangement less pronounced in *Chen*, *Philacte*, and *Anser*.

*Origin*.—Entire border of ischio-pubic fenestra medially, fascia of fenestra and inner surface of ischium.

*Insertion*.—Strong tendon through center of muscle running anteriorly and turning laterally through obturator foramen to external surface of femur above insertion of M. obturator externus in groove below crest of trochanter.

**M. GEMELLUS**

Small short muscle below and behind head of femur.

*Origin*.—Fleshy on pubis below acetabulum.

*Insertion*.—Fleshy on posterolateral angle of femur beneath insertions of *M. obturator externus* and *M. obturator internus*.

**M. ILIACUS**

Small short muscle below and in front of head of femur.

*Origin*.—Fleshy from small area on ilium beneath origin of *M. gluteus minimus*.

*Insertion*.—Fleshy on medial surface of femur just below head.

**M. AMBIENS**

Flat superficial muscle on medial surface of thigh.

*Origin*.—Fleshy on prepubis and pubis below obturator foramen; and extending, on pubis, about 5 mm. farther posteriorly in *Nesochen*, *Phalacte*, and *Branta c. minima* than in *Branta nigricans*. *Anser* similar to *Branta nigricans*, although actual width of origin greater; width of origin in *Chen* slightly greater than in *Nesochen*. In *Phalacte*, although width of origin great, posterior part of muscle poorly developed.

*Insertion*.—Long compact tendon crossing surface of patella from medial side to external side (yet beneath surface fascia of knee joint); passes beneath belly of *M. flexor perforatus indicus secundus pedis*, there broadens and serves as point of origin for lateral heads of *M. flexor perforatus annularis primus pedis*, *M. flexor perforatus medius primus pedis*, and *M. flexor perforatus indicus primus pedis*. In *Phalacte*, *Anser*, and *Chen*, *M. flexor perforatus medius secundus pedis* also attaches to tendon of *M. ambiens*.

**M. VASTUS INTERNUS**

Moderately small muscle closely applied to medial surface of femur.

*Origin*.—Fleshy from medial surface of femur; beginning slightly anterior to and beneath head and extending distally the length of shaft. Less extensive anterior to head in all others, *Branta* excepted. Area of origin on shaft broadest in specimens numbers 1 and 3 of *Nesochen*; juvenal *Nesochen* (number 4) about as in *Branta c. minima*, other forms with relatively narrower areas.

*Insertion*.—Strong compact tendon to scar at junction of inner cnemial crest with edge of articular surface of head of tibiotarsus.

**M. GASTROCNEMIUS**

Large thick muscle consisting of three well-separated parts, the two larger of which lie on medial and lateral surfaces of upper part of tibial segment.

*Origin*.—External head, tendinous on external condyle of femur and posterolateral angle of shaft proximally a total width of 14.5–15.8 mm. in *Nesochen*; 14.5 in *Anser*; 14.0 in *Branta c. minima*; 13 in *Chen*; 12.5 in *Phalacte*; 12 in *Branta nigricans*; heavy fascia of distal outer surface divided into two distinct points in *Nesochen*, especially well developed in specimen no. 1 (see fig. 3); no indication of this in *Chen*, *Phalacte*, and *Branta*; *Anser* shows trace of division. *Branta c. minima* has partial bipennate structure which is lacking in *Branta nigricans* and in other forms.

Tibial head, fleshy on medial surface of inner cnemial crest, medial margin of head of tibiotarsus, and, twisting around knee joint, from fascia covering patella.

Medial head, short tendon on extreme proximal edge of internal condyle of femur medial to insertion of *M. adductor*.

*Insertion*.—Delicate tendon of medial head is applied to lateral posterior face of distal part of belly of tibial head and runs on surface to merge with strong tendon of tibial head. Tendon of external head joins common tendon of tibial and medial heads just proximal to heel to pass as heavy thickened tendon over heel and attach to hypotarsal ridges, chiefly on innermost; fascia continuing from this point forms envelope over tendons of posterior aspect of tarsometatarsus and foot; a thickened part of fascia passes to base of free metatarsal one of hallux beneath tendon of *M. extensor hallucis brevis*; this attachment does not

appear to afford movement of metatarsal of hallux as it is opposed by ligament distally from base of metatarsal to end of second metatarsal.

#### M. SOLEUS

Small narrow muscle on posterior side of tibial segment beneath medial head of *M. gastrocnemius*.

*Origin*.—Fleshy from narrow area on posteromedial surface of tibiotarsus, beginning just beneath head and extending to point opposite and lateral to insertion of *M. semitendinosus*.

*Insertion*.—Long delicate tendon extending about two-thirds length of tibiotarsus to attach to medial margin of tibial cartilage lying in intercondylar sulcus of tibiotarsus.

#### M. PERONAEUS LONGUS

Thin extensive sheath of muscle on lateral surface of lower leg adjoining tibial head of *M. gastrocnemius* anteriorly.

*Origin*.—Heavy fascia on anterolateral aspect of knee joint, fascia from inner cnemial crest and fibula, and surface fascia of *M. tibialis anticus* and *M. flexor perforatus indicus secundus pedis*.

*Insertion*.—Tendon to heel which divides proximal to tibial condyles, one tendon with heavy fascia running to tibial cartilage, the other coursing over external surface of external condyle and hypotarsus to posterior side of tarsometatarsus to join tendon of *M. flexor perforatus medius primus pedis* about one-third length of tarsometatarsus from proximal end. Fascia of division to tibial cartilage and tendon narrower in other geese.

#### M. TIBIALIS ANTICUS

Two-headed muscle lying beneath *M. peronaeus longus* on anterior side of tibiotarsus.

*Origin*.—Lateral head, small tendon on anterior surface of external condyle of femur, running under patella to become fleshy beneath *M. flexor perforatus indicus secundus pedis* and, distally, to join fascia of anterior head in pennate fashion. In *Anser* and *Philacte* tendon gives way to fleshy part while still in contact with condyle.

Anterior head, fleshy on outer surfaces of inner and outer cnemial crests and slightly on medial surface of outer crest beneath origin of *M. peronaeus longus*; also on ventrolateral margin of patella.

*Insertion*.—Tendon through tendinous bridge on anterior surface of distal end of tibiotarsus to tubercle on medial side of anterior face of tarsometatarsus below head.

#### M. EXTENSOR LONGUS DIGITORUM

Single-headed bipennate muscle on anterior face of tibiotarsus beneath *M. tibialis anticus*.

*Origin*.—Fleshy from outer surface of inner cnemial crest, entire fossa between crests, and anterolateral surface of shaft of proximal half of tibiotarsus.

*Insertion*.—Central tendon, to which fibers attach bipennately, beginning proximally almost on level with cnemial crests; in other forms tendon weaker and slightly less extensive proximally; tendon without fleshy attachments continues along distal third of tibiotarsus to run beneath bony supratendinal bridge of tibiotarsus to anterior surface of tarsometatarsus through a tendinous loop distal to head of tarsometatarsus and on down anterior face of bone. Tendon divides into three; slightly farther distally inner subdivision itself divides into two; thus, four tendons produced. Of these (1) innermost runs to anterior ridge of second digit, perforating branch of tendon next lateral, and extends as compact tendon as far as second phalanx; beyond this, becomes fascia of anterior surface of digit. Next lateral tendon (2) branches at end of tarsometatarsus at sharp angle, to attach (a) to extreme base of second digit and (b) to base of third digit. Next to outermost tendon (3) runs to outer surface of base of third digit and distally to midanterior ridge of digit. Outermost tendon (4) runs to anterior face of digit four. Principal variation occurs in *Branta c. minima* in which outermost tendon is weak and fully fused with tendon next medial at base of toes; third and fourth tendons in others distinct, although joined by strong fascia.

**M. TIBIALIS POSTICUS**

Small slender muscle lying chiefly between and anterior to fibula and tibiotarsus.

*Origin*.—Fleshy on distal two-thirds of fibular crest of tibiotarsus, adjoining part of fibula, free shaft of fibula distally and interosseous membrane; in *Chen* and *Anser* on distal one-half of crest only.

*Insertion*.—Relatively large tendon running over anterolateral surface of external condyle of tibiotarsus to attach to posterolateral angle of head of tarsometatarsus.

**M. FLEXOR PERFORATUS INDICUS SECUNDUS PEDIS**

Single partly pennate muscle, partly exposed on lateral surface of lower leg between external head of *M. gastrocnemius* and *M. peroneus longus* (fig. 3).

*Origin*.—Short aponeurosis on lateral surface of external condyle of femur beneath external head of *M. gastrocnemius* and, somewhat separately from condylar attachment, by fascia to external surface of distal margin of patella in common with fibers of *M. flexor perforatus medius secundus pedis*.

*Insertion*.—Tendon on posterior margin of belly; tendon free of fleshy part for at least distal third of tibiotarsal segment, running over posterior medial surface of heel and over hypotarsus in groove just lateral to most medial calcanial ridge to base of digit two; tendon here perforates tendon of *M. flexor perforatus indicus primus pedis* and divides to attach on either side of base of second phalanx.

**M. FLEXOR PERFORATUS MEDIUS SECUNDUS PEDIS**

Single bipennate muscle beneath *M. flexor perforatus indicus secundus pedis*.

*Origin*.—Tendon to tendinous and ligamentous sheath that joins head of tibiotarsus and external condyle of femur, margin of patella with *M. flexor perforatus indicus secundus pedis*, and fleshy on external surface of fibula in region of insertion of *M. biceps femoris* and extending distally slightly beyond region of fibular crest of tibiotarsus; no direct attachment to tendon of *M. ambiens*, but *ambiens* bound to tendinous and ligamentous sheath just distal to origin of this muscle on this same sheath. In *Phalacrocorax*, *Anser*, and *Chen* junction of this muscle with sheath coincides with junction of *ambiens*; hence, action of *ambiens* must be transmitted to this part of this flexor; this association with *ambiens* especially pronounced in *Anser* and *Chen* where a few muscle fibers actually attach to tendon of *ambiens*.

*Insertion*.—Fibers converge bipennately to tendon that runs over posteroexternal surface of heel and in extreme lateral groove of hypotarsus; it is joined by weak vinculum from tendon of *M. flexor perforatus medius primus pedis*; tendon perforates that of *M. flexor perforatus medius primus pedis* in middle of base of phalanx of digit three to divide and attach on either side of base of third phalanx.

**M. FLEXOR PERFORATUS ANNULARIS PRIMUS PEDIS**

Distinctly double muscle beneath *M. flexor perforatus indicus primus pedis*; medial head joins lateral head as tendon at middle of belly of lateral head, to run along margin of belly and merge with tendon of lateral head to form common tendon of insertion.

*Origin*.—Medial head, fleshy on popliteal area of femur external to medial head of *M. gastrocnemius* and extensively from surface of medial head of *M. flexor perforatus medius primus pedis*. Lateral head, tendon in common with lateral head of *M. flexor perforatus medius primus pedis* which is continuous with tendon of insertion of *M. ambiens*; lateral head also by tendon to tendinous and ligamentous sheath that joins head of tibiotarsus and external condyle of femur.

*Insertion*.—Common tendon courses over heel and hypotarsus on external side to base of fourth digit; at this point it splits into three subequal divisions; lateral division attaches to base of second phalanx externally; innermost division attaches to plantar surface of base of fourth phalanx; tendon of *M. flexor perforans digitorum profundus* passes between middle and innermost division.

**M. FLEXOR PERFORATUS MEDIUS PRIMUS PEDIS**

Distinctly double muscle, the two parts lying beneath corresponding parts of *M. flexor perforatus annularis primus pedis*. In *Nesochen*, two entirely separate divisions each give rise to tendon; two tendons bound loosely to one another, finally joining just proximal to heel. In *Branta*, *Anser*, and *Chen* bellies of two divisions fuse loosely; tendons bound closely together throughout length, although double nature readily visible; complete fusion of tendons occurs several millimeters proximal to heel. In *Philacte* two heads fuse almost completely, so that division between them difficult to ascertain. In all forms an indication of double tendon remains where tendon passes over heel (fig. 5).

*Origin*.—Medial head, beneath corresponding head of *M. flexor perforatus annularis primus pedis* on popliteal area of femur; lateral head, tendon of *M. ambiens* in common with *M. flexor perforatus annularis primus pedis*.

*Insertion*.—Tendon passes, singly, to base of third digit, giving off vinculum to *M. flexor perforatus medius secundus pedis*; tendon joined by lateral tendinous insertion of *M. peroneus longus*; perforated at base of third digit by the two deeper flexor tendons of this digit to attach on either side of base of second phalanx.

**M. FLEXOR PERFORATUS INDICUS PRIMUS PEDIS**

Single muscle beneath and between divisions of *M. flexor perforatus medius primus pedis*.

*Origin*.—Fleshy from aponeurosis of more superficial flexors attaching to popliteal area of femur, by tendon on tendinous and ligamentous sheath that joins external condyle of femur and head of tibiotarsus, and fleshy to tendon of *M. flexor perforatus medius primus pedis* which is continuous with tendon of *M. ambiens*.

*Insertion*.—Fibers bipennately attached to tendon which continues as free tendon for distal one-third of length of shaft of tibiotarsus in *Nesochen*; in all other forms, especially *Branta nigricans*, however, belly restricted proximally to about one-half length of tibiotarsus; in all forms tendon courses over heel and through most lateral of two complete bony canals of hypotarsus; attaches to lateral surface of base of first phalanx of digit two in *Branta* and *Anser*; in *Nesochen* a strong flat tendon, not as definitely outlined as other tendons, branches and passes to medial surface of first phalanx; deep tendons of this digit perforate between this flat tendon and compact round tendon; in *Branta* medial tendon apparently represented by thin delicate fascia. In *Chen* a tendinous bridge covers deep tendons, the bridge not arising as branch of tendon of *M. flexor perforatus indicus primus pedis*; only connection of bridge to latter is vinculum sloping distally from bridge to tendon; insertion not studied in *Philacte*.

**M. FLEXOR LONGUS HALLUCIS**

Small single partly pennate muscle beneath long flexor muscles of other digits. Fleshy part shorter in *Branta c. minima*, *Philacte*, *Anser*, and *Chen* than in *Nesochen*; in *Branta nigricans* still shorter (fig. 5).

*Origin*.—Fleshy between condyles of femur distal to attachments of other flexors in popliteal area.

*Insertion*.—Tendon passes over external side of hypotarsus in deep bony groove just lateral to complete bony canals of this region; tendon gives off small branch to plantar base of ungual phalanx of hallux; remainder of tendon joins tendon of *M. flexor perforans digitorum profundus*, thus acting in common with it.

**M. POPLITEUS**

Small short muscle lying deep against tibiotarsus and fibula.

*Origin*.—Fleshy from posterolateral surface of tibiotarsus just below head.

*Insertion*.—Short tendon on posteromedial surface of head of fibula.

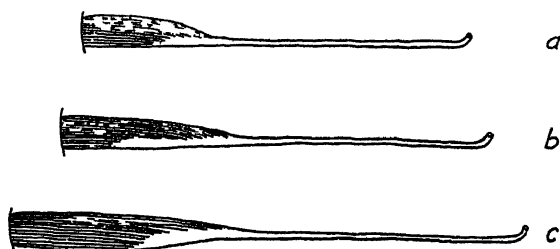
**M. FLEXOR PERFORANS DIGITORUM PROFUNDUS**

Bipennate muscle, deep on posterior side of lower leg distal to *M. popliteus*.

*Origin*.—Lateral head, fleshy, distal to insertion of *M. popliteus* on posterior surface of head of fibula; medial head, fleshy on posterolateral surface of tibiotarsus beneath distal

margin of origin of *M. popliteus*; heads merge about 2 cm. from head of fibula with fleshy attachments continuing distally on shaft of fibula and on posterior surface of tibiotarsus nearly to junction of fibula with shaft of tibiotarsus.

*Insertion*.—Fibers converge bipennately on tendon that continues free of fleshy parts for distal one-third of tibiotarsus; tendon runs in deep layer of tendons on medial surface



*Nesochen sandvicensis*



*Branta nigricans*

Fig. 5. *a, b, c.* Comparison of *M. flexor hallucis longus* to show lengths of bellies. *a, Branta nigricans*; *b, Branta canadensis minima*; *c, Nesochen sandvicensis*. All  $\times \frac{1}{2}$ .

Below. Comparison of *M. flexor perforatus medius primus pedis*. Left legs,  $\times \frac{1}{2}$ . *M. flexor indicus primus pedis* and ligamentous loop for *M. biceps femoris* show between heads of *M. flexor medius primus pedis*.

of heel through most medial complete bony canal of hypotarsus to be joined by main division of tendon of *M. flexor longus hallucis*; common tendon divides slightly proximal to base of hallux into three tendons each running to one of major digits (2, 3, and 4) and perforating tendons of primus and secundus groups of flexors to attach on plantar bases of ungual phalanges; distal to insertions of shorter flexor tendons, tendons of this muscle bound to digits by heavy connective tissue.

*M. EXTENSOR BREVIS DIGITI IV* (Gadow)

Small bipennate muscle closely applied to anterior aspect of tarsometatarsus. Fleshy part much more restricted in *Branta*, *Phalacrocorax*, *Anser*, and *Chen* than in *Nesochen*.

*Origin*.—Fleshy from lateral side of anterior face of tarsometatarsus for distal half of segment.

*Insertion*.—Strong tendon passing into intermetatarsal foramen to pierce, in a distal direction, the bridge joining metatarsals three and four distal to foramen; attaches to medial margin of base of first phalanx of digit four; tendon much weaker in other forms.

No muscular tissue seems to be present to represent the short flexors of some birds that arise from the tendons of the *M. flexor hallucis longus* and the *M. flexor perforans digitorum profundus* to pass to the bases of the digits.

#### **M. FLEXOR HALLUCIS BREVIS**

Vestigial muscle on posteromedial side of tarsometatarsus.

*Origin*.—Posterior surface of shaft of tarsometatarsus as delicate thread of muscle fibers; muscle tissue scarcely visible in *Branta* and *Chen*; not visible in *Anser*; not studied in *Philacte*.

*Insertion*.—Very small tendon on plantar base of first phalanx of hallux.

#### **M. ADDUCTOR DIGITI II (Gadow)**

Vestigial muscle on posterior side of tarsometatarsus.

*Origin*.—Posterior surface of shaft of metatarsus as delicate thread of muscle fibers. Muscular tissue scarcely visible in *Branta*, *Anser*, and *Chen*; not studied in *Philacte*.

*Insertion*.—Small tendon on lateral protuberance of base of first phalanx of digit two.

#### **M. EXTENSOR HALLUCIS BREVIS**

Extremely small muscle on medial surface of tarsometatarsus. Although well defined in *Nesochen* and distinct, but slightly smaller, in *Anser* and *Chen*, fleshy fibers in *Branta* scarcely visible to naked eye, these being replaced by connective tissue (muscle not preserved for study in *Philacte*).

*Origin*.—Fleshy on shaft of tarsometatarsus medially, about midway between hypotarsus and base of hallux.

*Insertion*.—Delicate tendon to anteromedial base of hallux and extending along medial surface to ungual phalanx. Tendon extremely small in *Branta*.

#### **M. ABDUCTOR DIGITI IV (Gadow)**

Extremely small muscle on posterolateral surface of tarsometatarsus beneath long flexor tendons; pennate structure. Muscle best developed in *Nesochen*; distinctly smaller in *Branta*; not studied in *Philacte*.

*Origin*.—Fleshy from posterolateral surface of tarsometatarsus beginning distal to hypotarsus and extending length of metatarsus.

*Insertion*.—Marginal tendon to anterolateral surface of base of first phalanx of digit four.

#### **M. ABDUCTOR DIGITI II (Gadow)**

Extremely small muscle on medial surface of tarsometatarsus.

*Origin*.—Fleshy on distal third of medial surface of tarsometatarsus; on distal fourth in *Branta*, *Anser*, and *Chen*; not studied in *Philacte*.

*Insertion*.—Short tendon on distal outer margin of belly running to anteromedial surface of base of first phalanx of second digit.

#### **M. EXTENSOR BREVIS DIGITI III (Gadow)**

Extremely small muscle on anterior surface of tarsometatarsus; may represent both *M. extensor medius brevis* and *M. extensor proprius* mentioned by Beddard (*op. cit.*, p. 103). No muscle fibers visible in *Chen* and little or none in *Branta* and *Anser* in decided contrast to *Nesochen*; not studied in *Philacte*.

*Origin*.—Fleshy on anterior surface of distal part of tarsometatarsal shaft.

*Insertion*.—Relatively short tendon over trochlea to anterior spine on base of first phalanx of digit three. Tendon present in all forms despite lack of muscle fibers.

### QUANTITATIVE COMPARISON OF MUSCLES AND MUSCLE FUNCTION

Some of the most pronounced specific differences in the musculature of geese are of a purely quantitative nature. Muscle bulk was determined by immersion in water. Readings were taken to one-tenth of a cubic centimeter. With the exception of certain small muscles of the foot and the obturator group, all muscles of the hind limb were measured. Many of the muscles have a bulk of two or more cubic centimeters so that the precision of the measurement is adequate.

Quantitative relations of the hind limb as a whole to the entire body were determined by removing the leg from the pelvis (skin removed except from tarsus and foot). Both weight and bulk were taken. Where total leg bulk

TABLE 1  
RELATIVE DEVELOPMENT OF THE LEG

|                                                                    | Nesochen<br>no. 1 | Nesochen<br>no. 3 | Nesochen<br>no. 4 | Branta c.<br>minima | Branta<br>nigricans | Philacte | Anser | Chen  |
|--------------------------------------------------------------------|-------------------|-------------------|-------------------|---------------------|---------------------|----------|-------|-------|
| Per cent of total leg<br>weight of body weight.                    | 8.98              | .....             | .....             | 7.20                | 4.59                | .....    | 6.99  | 7.32  |
| Per cent of total bulk of<br>leg muscles of body<br>weight.....    | 5.27              | .....             | 4.74              | 4.45                | 2.10                | 2.99     | 3.88  | 3.64  |
| Per cent of total bulk of<br>leg muscles of total leg<br>bulk..... | 65.87             | 57.34             | .....             | 67.31               | 64.34               | .....    | 60.57 | 53.84 |

could not be determined, sums of the bulks of the muscles measured were compared to total body weight. Table 1 shows the relatively large leg of *Nesochen*. The interspecific difference in *Branta* is striking, with *B. nigricans* showing wide divergence from the other geese that evidently is to be associated with its strong maritime proclivities and consequent large amount of time spent in the water unsupported by the legs. The leg of *Philacte* is proportioned along similar lines to that of *nigricans*, but not to so extreme a degree.

Table 1 also illustrates the relative development of the muscles in the various individuals by means of the ratio of leg-muscle bulk to total leg bulk. The difference shown in the one-year-old and six-year-old specimens of *Nesochen* points to age as the principal factor in the variation of this ratio. The low figure for *Chen* I cannot account for. It can be stated with some assurance that there are no large variations interspecifically in the bulk of the leg musculature out of proportion to the other parts of the limb. From the appearance of the juvenal *Nesochen* I surmise that its percentage of muscle bulk would have been even lower than that of the yearling example had figures been available.



The difficulties that beset an analysis of muscle function have been well set forth in the writings of A. B. Howell (1926, pp. 173-216), and Wright (1928, pp. 3-26). The points which they make have been fully considered in my analysis of limb mechanics. Approaching the problem of function by the anatomical method, it is not possible to solve questions concerning the nature of the nervous coördination of the various muscle elements. Beavor (1904, p. 3) has pointed out that through dissection and experimental stimulation one learns what a muscle *may* (or *can*) do in contradistinction to what it actually does in life. Yet there is value in determining what a muscle *may* do, especially when the mechanical situation indicates that it acts in a different fashion and degree in different species. Especially important factors in the mechanical equation are the synergist relations and the so-called tendon and ligamental actions.

Three things simplify problems of function in the geese to some degree. First, in this group, as in all birds, the limb is much less flexible than those of many mammals and accordingly pronation, supination, and rotation at the knee and ankle are reduced or entirely lacking. The muscles function chiefly as extensors or flexors, with the exception of those of the femoral segment where the usual ball-and-socket joint allows freedom of movement. Second, in the geese we are dealing with a series of closely related forms and the structure within the group is relatively uniform. It can be assumed that the coördination of impulses follows a similar instinctive pattern in the different species, that muscle for muscle the histologic structure is similar, and that quality of nervous impulse to the muscle, aside from individual variation, is fairly stable. Third, the attachments of muscles of the hind limb are somewhat more restricted and definite than those in mammals of generalized type and so are, in some instances, more amenable to a fairly exact analysis of lever action.

The bulk is of course proportional to the work (force through distance) of which the muscle is capable. Force is proportional to the greatest cross section and the distance proportional to the length along the fibers. In pennate and bipennate muscles, force is increased at the expense of distance through which the action can take place. At the same time efficiency is lost in the components of force lateral to the tendon brought about by the direction of the fibers in such muscles. Bipennate structure permits a muscle to occupy a long narrow space and yet develop a great degree of power.

#### MOVEMENT OF LIMB SEGMENTS IN RUNNING AND SWIMMING

To appreciate the rôle played by the individual muscles one must clearly understand the movements of the limb segments in both propulsive and recovery strokes of running and swimming. Diagrams have been prepared (fig. 6) to aid in visualizing the motion; these are based upon field studies made by Mr. James Ashley and myself, and upon photographs taken by Ashley of walking and running geese. For further discussion of limb mechanics, especially with regard to joints, see Stolpe (1932).

The propulsive stroke in running or walking begins when the foot strikes the ground. At this time the toes are extended, tarsometatarsus extended, tibiotarsus partly flexed and femur flexed. As the stroke proceeds, the leg

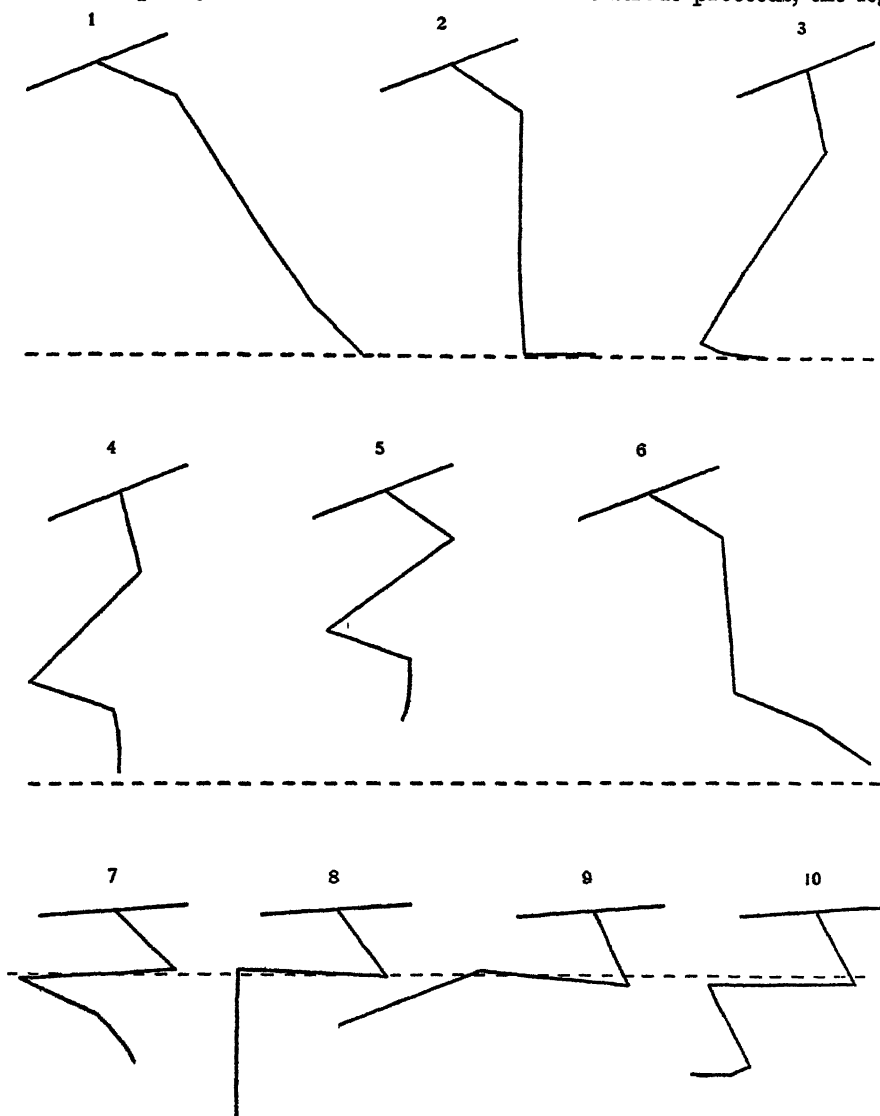


Fig. 6. 1-6, Diagrams of positions of limb segments in right leg of *Branta canadensis* in walking: 1-3, beginning, middle, and end of propulsive stroke; 4-6, beginning, middle and end of recovery stroke.

7-10, Positions of limb segments in swimming: 7-9, beginning, middle, and end of propulsive stroke; 10, recovery stroke.

swings backward with tibiotarsus flexing and toes bending forward until the tibiotarsus and tarsometatarsus are in a vertical line. In the last half of the stroke the femur extends, the tibiotarsus extends, and the base of the toes leaves the ground, especially if the bird is running, not walking.

The recovery stroke begins with a distinct flexion of the tarsometatarsus and tibiotarsus and a return of the toes to a straight or slightly flexed position. The foot thus is lifted from the ground. The femur now begins to flex, swinging the leg forward; the tibiotarsus, tarsometatarsus, and toes are further flexed, except in *Nesochen*, so as to keep the foot clear of the ground and bring the tarsometatarsus into an almost horizontal position. As the limb swings far forward the tibiotarsus is partly extended and the tarsometatarsus and toes are completely extended.

In swimming, the femur is nearly static in relation to the sacrum, and the tibiotarsus is only slightly flexed on the propulsive stroke, even in vigorous swimming. Most of the motion is at the heel, so that the tarsometatarsus is strongly flexed in recovery and extended in propulsion. The toes are flexed during the early recovery stroke to become partly extended for the beginning of the propulsive stroke. They become fully extended in the later phases of propulsion.

#### DIFFERENCES IN LEG ACTION OBSERVED IN GEESE

Some observations made principally by James Ashley (MS) on the mode of walking in *Branta c. canadensis*, *Anser albifrons*, and *Chen hyperborea* and my own observations on *Branta c. minima* and *Nesochen* are here given. They should serve to clarify certain differences in mode of walking not made apparent in the earlier section on natural history.

The length of the stride was found to be long in *Chen* and *Branta c. minima*, slightly shorter in *Branta c. canadensis* and shortest in *Anser*. In *Nesochen* it appeared to be longer than in *Chen* (see p. 4). The swinging of the body from side to side is least in amount in *Nesochen* and *Branta*, more in *Chen* and most in *Anser*. Toeing-in is least in *Nesochen*, slightly more in *Chen*, still more in *Branta c. canadensis*, and most in *Anser*. The angle that the leg makes with the ground when beneath the acetabulum is greatest in *Anser*, that is, the leg slopes medially toward the ground to the greatest degree. In *Branta c. canadensis* it is set more nearly at right angles to the ground; in *Branta c. minima* and *Chen* it is still straighter and in *Nesochen* straightest.

These differences indicate that there is more efficient leg action with longer stride and less lateral motion of the limb away from the line of progress in *Nesochen* than in the others. *Branta c. minima* and *Chen* stand next to *Nesochen* in efficiency; *Branta c. canadensis* is somewhat less efficient. *Anser* is the least efficient of the forms observed.

#### COMPARISON OF ACTIONS AND WORK CAPACITIES OF MUSCLES

After experimentation with methods of comparing bulks of individual muscles, the ratio of the muscle to the sum of leg muscles measured was adopted as the most widely useful. It allows one to compare, in the different species, the importance of each muscle as a unit in the mechanism. In certain instances in which muscles act directly against the weight of the body the ratio of muscle to body weight is significant. Specimen no. 3 of *Nesochen* was used as most nearly representative of average bulk relations in the genus (see p. 39; fig. 10).

*Muscles moving the femur; one-joint group from sacrum to femur.*—Two of these muscles, the *M. gluteus medius* and *M. gluteus minimus*, are similar in their actions. They are able to flex the femur very slightly. In so doing they work with an extremely short power arm, especially the gluteus medius because of its insertion almost opposite the fulcrum of the head of the femur. To cause flexion they would have to be opposed at the time to some degree by the two obturator muscles and perhaps by the gemellus, otherwise their attachment on the outer surface of the femur would produce a rotation of the

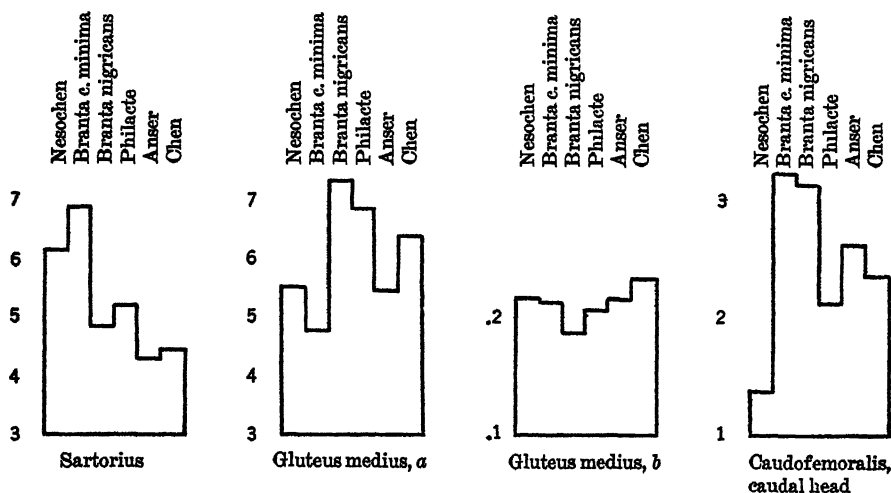


Fig. 7. Histograms showing relative sizes (bulk) of leg muscles in different kinds of geese. Numbers represent per cent of total leg muscle bulk, except for gluteus medius, b, in which numbers represent per cent of body weight.

bone. This latter is doubtless the major function of the muscles. The angle at which the aponeurosis attaches to the bone suggests rotation rather than flexion. Contraction of the minimus would cause rotation around the axis of the shaft, that of the medius a similar rotation, but it also would pull the trochanter inward and hence abduct or throw the knee outward.

By group action of these gluteals and the obturators the femur is probably held in fixed position with regard to rotation and perhaps statically in a condition of partial flexure while other movements of the leg are carried on, thereby bracing the base of the limb in action as well as maintaining posture. There may be a combined rotation and flexion effected while the limb moves forward that causes the familiar toed-in position of the foot and the swinging of the foot in an arc during recovery. The shortness and breadth of the muscles is in agreement with the short range of action and large amount of power necessary for the movements indicated and for postural functions.

The bulk of the *M. gluteus medius* is appreciably less in *Nesochen*, *Anser*, and *Branta c. minima* than in the other forms (see fig. 7). This difference I believe to be the result largely of the greater development of the leg in the former group, so decreasing relatively the bulk of this muscle. The gluteus medius appears to be limited by the size of the iliac fossa, which, although

some variations in shape have been noted, corresponds closely in size to the bulk of the entire animal. Thus, the muscle compared to total body weight is without important variations as may be seen in figure 7. The bulk of the gluteus minimus was not taken.

The differences in the origins mentioned on page 8 point to slightly different functional capabilities. The more laterally directed iliac surfaces of *Nesochen* and the downwardly deflected anterior part bring the fibers of the gluteus medius into a more horizontal position than in the other forms and permit rotation as in the gluteus minimus but with a loss of abducting power. Greater anterior extent in *Nesochen* allows greater range of action of the medius. A comparable situation obtains in the gluteus minimus where the origin extends progressively farther anteriorly in *Anser*, *Philacte*, *Chen*, *Branta* and *Nesochen*. Thus, although *Nesochen* does not in practice rotate the limb as much as do other geese, it seems to be capable of greater flexibility in the matter of rotation.

The M. obturator externus and M. obturator internus are antagonistic to the two gluteal muscles just discussed. The obturator externus opposes the slight flexor and considerable rotating action of the gluteus minimus. Its extensor action cannot be considered of importance, especially since more advantageous and powerful extensors attach distally to it on the femur. The slightly higher insertions in *Chen* and *Anser* would reduce, relatively, the extensor power in these forms. The obturator internus opposes the rotation of the femur around its axis produced by the gluteus medius and also the latter's dorsomedial component force on the trochanter; it serves to pull the trochanter out and down to throw the knee medially. Lesser power of the internus is indicated in *Chen*, *Philacte* and *Anser* by less pronounced bipennate arrangement.

The M. adductor longus and M. adductor magnus serve for extension of the femur rather than for adduction, as their names imply. Their origin is almost directly posterior and dorsal to their insertion so that they could not adduct the limb when it is in normal vertical position. The great breadth of origin and consequent variation in the angle at which the parts run to their insertion causes the anterior and posterior regions to operate with different mechanical advantages. The posterior part runs to the femur at an angle approaching the right angle so that nearly all its power is effective in motion. A large component of the anterior part, however, acts to thrust the head of the femur dorsally in the acetabulum, less of its power serving for femoral extension. The component for the thrust on the head increases greatly when the femur is far forward in flexure. The anterior part is, then, more involved in maintaining posture and is effective in the movement of the femur through only a short distance with but little power, though with good speed. The posterior part is chiefly responsible for the power needed in femoral extension and operates effectively through a wide range of movement.

Active contraction of the muscle must be a factor in running and jumping, aiding in extending the leg and thrusting it back to oppose body inertia.

Since in swimming, femoral extension is limited, the adductor group would serve most importantly as braces, merely preventing the femur from flexing under the action of the *M. biceps femoris* and *M. semitendinosus*. This same static action, holding the femur in resistance to flexion, is necessary while standing when the femur is not perpendicular to the ground; the adductors are of course aided in this by several other muscles. Conceivably the adductors operate also in conjunction with the *M. sartorius*, for if the latter is to serve for tibial extension alone, the adductors or *M. caudofemoralis* must counteract the flexing action of the *sartorius* on the femur. In similar manner by active contraction and extension of the thigh, the adductors can actively reinforce the tibial extension of the *sartorius*, the latter exerting the so-called tendon action because extension of the femur by the adductors puts it under stress.

It is perhaps to be expected that the adductors, capable of serving importantly in numerous types of leg movements show no significant specific variations in bulk. Almost the entire range of interspecific difference was found to be included in the range of individual variation in *Nesochen*. There is clearly a greater development of the posterior part in *Nesochen* and *Branta c. minima*, especially in the older specimens of the former, the resultant power and range of action being important adjuncts to running ability. The angle that the posterior margin of the muscle makes with the femur when the latter is perpendicular to the sacrum does not vary importantly. The differences as a result of this variation (assuming muscle contraction equal) in the force component causing femoral extension, are in no instances greater than three per cent.

The iliac head of the *M. caudofemoralis* is entirely an extensor of the femur (there is no origin upon the tail). Its action is comparable with the more posterior parts of the adductor group and hence its relations to *sartorius* action and *biceps femoris* action are similar. It differs from the adductors in that the insertion is more proximal on the femur, so shortening the power arm in femoral flexion. Greater speed and less power result in comparison with the posterior parts of the adductors. The position of the insertion reduces the dorsal thrust component on the femur to a much lower figure in the *caudofemoralis*. The greater posterior extension of the origin in *Nesochen* permits greater range of femoral extension. The variations in bulk are not significant.

Some interspecific differences in the length of the power arm (head of femur to distal edge of scar of insertion) occur, but individual variation throws doubt upon the value of these. Two of three specimens of *Branta nigricans* have shorter power arms than all the other geese, but a third has a slightly longer arm than any of those of the land forms; in *Philacte* it is decidedly longer than in the land geese. If extension of the femur were an important element of the propulsive stroke of swimming one would expect the power arm in swimming forms always to be greater in order to aid in movement through the highly resistant medium.

The caudal heads of the *caudofemoralis* on the two sides of the body, if contracting simultaneously, must produce movement similar to that effected by the iliac head, balancing one against the other to prevent lateral motion of the

tail. However, it is difficult to visualize use of the muscles in this fashion in running because femoral flexion would alternate on the two sides. In swimming, the two muscles may operate simultaneously to brace the femur. Conceivably, other caudal muscles serve as synergists to the caudal heads when they are acting alternately, in order to prevent tail motion that might otherwise accompany leg movements.

A probable function of the caudal head is lateral motion of the tail, more or less independent of leg movements. In movements of the tail far to one side or the other a long muscle of this type would be especially advantageous. It is not known whether there are differences among geese in the wagging of the tail, but this habit is common in several of our North American species. In any event the pronounced variation in bulk between forms does not correlate with swimming habit such as might be expected if the caudal head were used as a brace for the femur in swimming movements. Instead, the variations seem to accord with the taxonomic arrangement of the species so that the two species of *Branta* are closely similar and distinguished clearly from the other forms. *Nesochen* likewise is set off from the others in this respect, but holds a position at the opposite extreme from *Branta* (see fig. 7).

The *M. gemellus* must function chiefly in posture. It is an adductor, but should be able to rotate the trochanteric region posteriorly to a limited degree. The *M. iliacus* is comparable in its action to the *gemellus* except that it rotates the trochanteric region anteriorly. The *M. gluteus anterior* is purely an abductor, but is weak like the *gemellus* and the *iliacus* and could not be effective in any power movements of the leg.

*Muscles moving femur and tibia; two-joint group from sacrum to tibiotarsus.*—The *M. sartorius* is a flexor of the femur and extensor of the tibiotarsus. It would appear to be of less importance as an adductor, since it can move the limb only slightly toward the axis of the body. The tendon action of the *sartorius* causing tibial extension as well as its active contraction to produce this result has been mentioned. With opposition from the tibial flexors it would cause femoral flexion alone. In running it should serve during the recovery stroke, bringing both the tibiotarsus and femur forward; only slight tibial extension and femoral flexion would be required in recovery in swimming. The muscle is not a factor in the power drive of swimming since the tibiotarsus flexes and the femur extends slightly in this act. In running, however, there is always some tibial extension and in jumping and climbing this is greatly augmented. In such actions the *sartorius* should aid the *M. extensor femoris* and *M. vastus internus* if opposed by femoral extensors. It can therefore serve both in recovery and in the power drive of extension when the bird is on land, but it can serve only in recovery in swimming.

The bulk of the *sartorius* is to be identified in this manner with running and jumping and the need for rapid recovery strokes in the former. The histogram (fig. 7) demonstrates the greater bulk in *Nesochen* and *Branta c. minima* compared with that of other geese. The variations in the origin do not alter importantly the leverage of *sartorius* action.

The M. ambiens is unique in that its tendon is continuous with the primus group of flexors of the toes. These latter are bound by a ligamentous sheath to the knee joint so that the ambiens cannot move the proximal ends of these muscles without pulling on this sheath. However, the sheath is not so arranged that a direct pull would move the knee without buckling the sheath in an incongruous manner. The ambiens, if acting simultaneously with the toe flexors, would adduct the thigh, exert a slight extensor force on the tibiotarsus, tend to rotate the anterior surface of the tibiotarsus inward, and reinforce toe flexion. Adduction and reinforcement of toe flexion are its principal uses; the former is probably largely static but would have to be carried on in continual balance with the state of tonus and contraction of the toe flexors. The ambiens cannot contribute greatly to the range of toe flexion because of the binding of the origins of the toe flexors to the knee. When the toe flexors are under severe stretch as in standing, in the latest phase of propulsion in running, or at the beginning of the swimming stroke, the ambiens could aid the flexors as a group and contribute power to the action of these muscles either to flex the toes or aid tarsal extension.

There is yet another function that the ambiens may perform in connection with toe flexors. This is its power to counteract the tibial flexion that is induced by the medial heads of these flexors through their origins on the popliteal area of the femur. Thus, by action of the lateral heads, medial heads, and the ambiens simultaneously, digital control without accompanying tibial movement may be had. This synergist function of the ambiens may be an important corollary of its connection with the toe flexors.

The numerous functional possibilities of the ambiens make it impracticable to speculate at length on the significance of differences in bulk. *Nesochen*, except for the juvenile, has a smaller ambiens than any of the other geese. This may be partly the result of great increase in bulk in some of the larger muscles, so dwarfing the ambiens by comparison. The relatively larger size in the juvenile bears this out. A comparable effect should be found in *Branta c. minima* which, however, is not to be found. The smallness of the ambiens in *Nesochen* is perhaps without functional significance; it cannot be associated definitely with walking or running unless it be connected with reduction of toeing-in (rotation).

The M. gluteus primus is both an extensor of the tibiotarsus and an abductor. Its extensor action should be the same as that of the M. extensor femoris. The gluteus primus is the only important abductor. It can cause this movement exclusive of extension, only when tibial extension is opposed by the biceps femoris and semitendinosus. Its bulk is greater in *Nesochen* and *Branta c. minima* (fig. 8) doubtless because of its action as an auxiliary of the extensor femoris which is relatively greatly enlarged in the running types.

The M. biceps femoris and M. semitendinosus are the main sources of power in tibial flexion. They can also cause femoral extension, especially when tibial flexion is opposed. In swimming, the power stroke of the limb is tarsal extension, with relatively little motion of the tibiotarsus, except perhaps in rapid



swimming. These muscles serve chiefly as braces during swimming to prevent tibial extension. The forcing of the foot through the water exerts a great force at the knee that tends to thrust the knee forward and to straighten it. To oppose this force and keep the limb in place the biceps and semitendinosus must contract with great power.

The biceps functions somewhat differently from the semitendinosus in that the tendinous sling makes its direction of pull on the tibiotarsus constant. With the tibiotarsus extended the sling has little effect, but in final stages of flexion the sling acts as a pulley, directing the force of contraction to bring about extreme flexion. Without this pulley, the biceps, after flexion had passed the right angle, would no longer flex efficiently, but would yield an increasingly greater component tending to pull the head of the tibia away from its articulation with the femur. No other muscle could act directly to prevent this although the ligaments of the joint would check it. With the loop arrangement there is always a component force directed to holding the tibiotarsus against the femur.

In the act of running, the biceps can serve in swinging the entire limb backward, acting in conjunction with the extensor femoris which prevents tibial flexion. The muscle is not used directly in jumping or the phases of running that require active limb extension.

A comparison of bulk shows the expected relatively great work capacity of this muscle in the swimming forms (fig 8). The weakness in *Chen*, apparently an efficient swimmer, I am unable to explain. In making this statement of comparison it should be kept in mind that power of the biceps in relation to *body weight* is not greater in the swimming forms, but actually less. In other words the great development of the legs in *Nesochen* has been a general one, with relatively greater or lesser development of certain muscles. The general increase in the leg has, so to speak, carried the biceps to a greater actual bulk development than in the swimming forms, not because *Nesochen* swims, but because certain balances and proportions among muscles of a limb must be maintained and because the biceps has a decided function in running. Such considerations do not negate the significance of the large size of the biceps in relation to that of other leg muscles in the swimmers such as *Branta nigricans*. Similar situations arise in other comparisons that follow where relative bulk is stated to be greatest in the weak-legged swimming forms, *Philacte* and *Branta nigricans*.

The variations in origin of the biceps do not seem to have functional significance as they are slight, and the direction in which the power is applied is controlled by the loop from the femur. The unusual insertion on the surface of the *M. gastrocnemius*, present generally in the Anatidae, likewise appears to have no great functional value, although it illustrates how muscles may shift insertions, eventually providing opportunity for important changes in mode of action. The position of the insertion upon the fibula, however, differs significantly among the genera discussed. Analysis of the lever action connected with tibial flexion by the biceps has been made. The power arm of the

lever was taken as the distance from the articular surface of the tibiotarsus to the most distal (usually highest) part of the scar of insertion on the fibula. The weight arm was considered to be the shortest distance between the articular surfaces at either end of the tibiotarsus. A ratio of the two arms indicates the efficiency of the lever, a greater power arm acting with greater force but less speed. The ratio between power arm and a longer weight arm, namely, tibial plus tarsal length, also was taken because the biceps may act to force the foot either through the water (late phase of propulsion) or against the ground when other muscles coöperate to maintain the tarsus extended. Average ratios in per cents for each species are as follows:

TABLE 2  
LENGTH OF POWER ARM IN BICEPS ACTION

| Species                                | Number of specimens | Per cent of tibial length |           | Per cent of tibial plus tarsal length |           |
|----------------------------------------|---------------------|---------------------------|-----------|---------------------------------------|-----------|
|                                        |                     | Average                   | Extremes  | Average                               | Extremes  |
| <i>Nesochen sandvicensis</i> . . . . . | 4                   | 20.95                     | 20.7-21.1 | 12.87                                 | 12.7-13.0 |
| <i>Branta c. minima</i> . . . . .      | 5                   | 22.20                     | 21.8-22.5 | 13.78                                 | 13.6-14.0 |
| <i>Branta nigricans</i> . . . . .      | 5                   | 22.04                     | 21.8-22.3 | 13.92                                 | 13.7-14.2 |
| <i>Philacte canagica</i> . . . . .     | 2                   | 22.15                     | 22.1-22.2 | 14.10                                 | 14.0-14.2 |
| <i>Anser albifrons</i> . . . . .       | 6                   | 24.00                     | 23.3-25.0 | 15.13                                 | 14.6-15.8 |
| <i>Chen hyperborea</i> . . . . .       | 6                   | 22.13                     | 21.8-22.6 | 13.63                                 | 13.5-13.8 |

Calculating the moments of force in these lever actions it may be shown that for a given unit of muscle pull, *Branta nigricans* develops 5.2 per cent (average) more force at the end of the tibiotarsus than does *Nesochen* or that *Chen* develops 5.9 per cent more force at the foot (base of toes) than does *Nesochen*. These are minimum differences between the island goose and the others. *Anser* may develop 17.5 per cent more force at the foot. This does not mean, taking actual bulk into account, that more force is generated in *Anser*, but only that per unit of force of contraction, *Anser* is 17.5 per cent more efficient. Conversely, *Nesochen* to an equivalent degree is more efficient in generating speed. By way of further comparison I have calculated that in the loon, *Gavia*, an extreme example of aquatic adaptation, 50 per cent more force per unit contraction is produced at the end of the tibiotarsus than is produced in *Nesochen*.

The table of calculations demonstrates, then, that the biceps lever arrangement is adapted to rapid movement (running) in contrast to power movements (swimming) to the greatest degree in *Nesochen*. The two species of *Branta*, and *Chen*, and *Philacte*, are similar in this respect, no one individual among them closely approaching *Nesochen*. *Anser* represents the opposite extreme, being set off from *Branta*, *Chen*, and *Philacte* to a degree comparable to that which sets off *Nesochen* in the opposite direction.

It is surprising to find the two species of *Branta* so similar with regard to leverage in view of pronounced swimming modifications in *nigricans*. It must

be concluded that the position of the biceps insertion is more conservative in its alterations and has no intrageneric modifications, even though other parts of the limb have undoubtedly been modified one way or another to fit the species for differing activities.

In considering the modifications of biceps insertion I cannot escape the thought that the differences in leverages are brought about as much through lengthening or shortening of the shafts of the leg bones as by shift of the insertion point in relation to the knee. Thus, elongation of the legs in *Nesochen*,

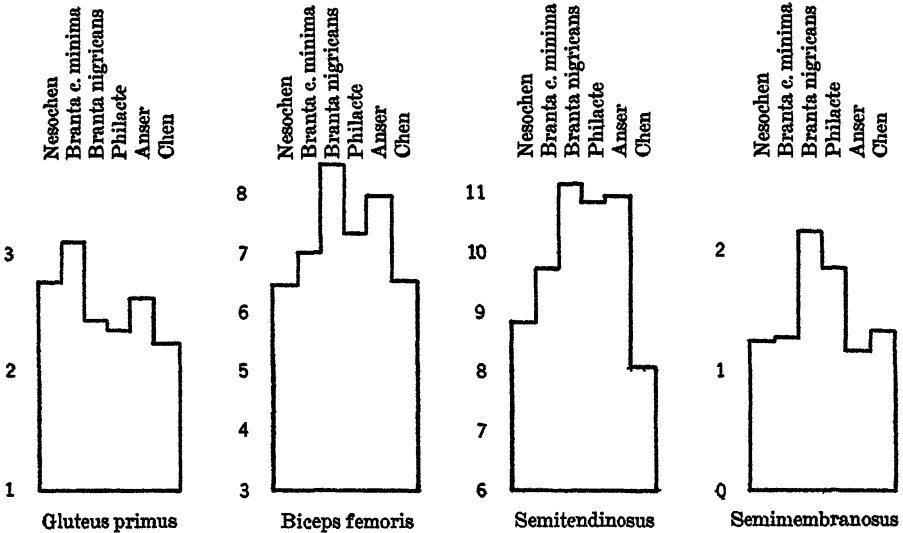


Fig. 8. Histograms showing relative sizes (bulk) of leg muscles in different kinds of geese. Numbers represent per cent of total leg muscle bulk.

especially in the shafts of the tibiotarsus and tarsometatarsus, would bring about the leverage characteristic of this form without an absolute shortening of the power arm of the lever. In like manner the short tarsometatarsus of *Anser* is a contributing factor in the relatively long power arm. The relatively long tarsometatarsus of *Chen* influences the ratio of lever arms in an opposite direction.

Unlike the biceps, the *M. semitendinosus*, after tibial flexion has gone past 90 degrees, tends to pull the tibiotarsus from the femur. This tendency is always counterbalanced by the action of the biceps running through its loop. The semitendinosus cannot function for flexion in the extreme late phase of this movement as can the biceps. In another respect the biceps and semitendinosus balance one another in that the former inserts on the fibula, the latter on the tibia at about the same level. Thus, they work in common to prevent tibial rotation, the fibula and tibiotarsus being fairly rigidly cojoined. Probably they seldom function separately to any great degree to produce rotation.

The slightly more posterior position of the origin of the semitendinosus (see p. 10) in *Philacte*, *Anser*, and *Chen* is a modification in the direction of greater power at the expense of speed. Greater post-acetabular extent of the pelvis is a concomitant modification.

The histogram for the semitendinosus (fig. 8) is closely similar to that for the biceps. This is to be expected in view of similar functions. Also the variations in bulk of the semimembranosus are similar (fig. 8), with the marked exception of *Anser*. The M. semimembranosus, with insertion in common with the semitendinosus, is merely an auxiliary of the latter. It could be effective only during the earlier phases of tibial movement because of its origin lower down on the pelvis nearer the tibial shaft. Perhaps it is at this position, with tibiotarsus well forward and semitendinosus pulling at a disadvantageous acute angle to the shaft, that an auxiliary like the semimembranosus is most needed. The three muscles, semimembranosus, semitendinosus, and biceps, in *Anser* show progressively smaller relative bulk in inverse proportion to the degree to which these muscles are concerned with the early stages of tibial flexion. This correlates with shorter stride and more swimming activity in *Anser*.

*Extensor of the tibiotarsus; one-joint group from femur to tibiotarsus.*—Among the larger muscles of the leg the M. extensor femoris is one of the simplest in action. Extension of the tibiotarsus is its sole function, for unlike its counterpart in mammals it has no attachment to the pelvic girdle. As is true of any of the extensors of the tibiotarsus, contraction of the extensor femoris is an aid to the biceps and semitendinosus in swinging the entire leg backward in walking. However, the extensor femoris and its auxiliary the M. vastus internus can aid in this manner without other complications such as femoral flexion (sartorius) or abduction (gluteus primus). For the upper limb segments the extensor femoris is the chief source of power in leaping, climbing, and the late phase of propulsion in running.

The differences in bulk are remarkable in this muscle and also highly significant because of the simplicity of function. The histogram (fig. 9) shows the extraordinarily great relative size in *Nesochen* and the weakness in *Branta nigricans*. Because the muscle in extending the tibiotarsus acts directly against the weight of the body, a comparison of bulk with body weight is important (fig. 9). This histogram is constructed with a unit value that stands in about the same proportion to the object of comparison (body weight) as does the unit in the first histogram. Even more pronounced is the development of the extensor in *Nesochen* in this latter comparison. These comparisons constitute the most instructive instance of differentiation in muscle power in the entire limb. Because the muscle can serve but slightly in swimming (recovery stroke) and since it is obviously of great use in jumping, climbing, and to a noticeable degree in running, it displays marked adaptation in *Nesochen* at one extreme and in *Branta nigricans* at the other. Also to be seen are the approach of *Philacte* to *Branta nigricans* in swimming adaptation and the slight, though definite, running adaptation of *Branta c. minima*.

The M. vastus internus must function in tibial flexion but its insertion at the junction of the cnemial crest and the articular surface makes its leverage much less powerful than that of the M. extensor femoris which attaches to the patella and so indirectly to the tip of the cnemial crest. Although the vastus

internus would appear to have chiefly an extensor function, it may serve to check tibial rotation caused by the ambiens. In its bulk it shows none of the modifications found in the extensor femoris so that it does not appear to be an element in adaptive modifications concerned with the power of tibial extension. The variations in bulk are slight.

*Muscles moving tarsometatarsus primarily; two-joint group from femur to tarsometatarsus.*—Both the *M. gastrocnemius* and its antagonist, the *M. tibialis anticus*, have parts taking origin on the femur with other parts arising solely

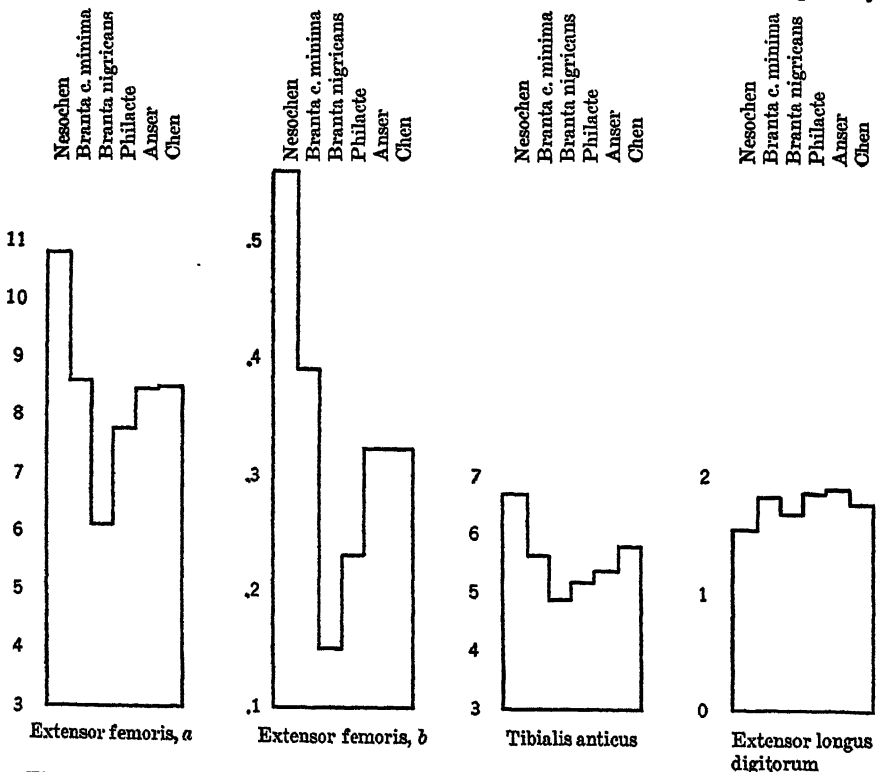


Fig. 9. Histograms showing relative sizes (bulk) of leg muscles in different kinds of geese. Numbers represent per cent of total leg muscle bulk, except for extensor femoris, b, in which numbers represent per cent of body weight.

on the tibiotarsus or patella which is functionally merely a continuation of the cnemial crest. The *M. tibialis anticus* serves as a tarsal flexor; contraction of the lateral head could also cause tibial extension. When this lateral division contracts, it puts under stress a number of muscles attached to the femur whose tendons course over the heel. Unless this stress be completely offset by relaxation of tonus, the stress would tend to flex the tibiotarsus. Probably the extensor action of the lateral head of the *tibialis anticus* is merely for the purpose of balancing this stress and is not important in major extension movements of the tibiotarsus.

The *tibialis anticus* is the only direct tarsal flexor and as such functions in the recovery strokes of swimming and running. Some differences exist in the

position of the tubercle for the insertion that make it desirable to calculate and compare the lever action. The distance from the proximal articular surface of the tarsometatarsus to the distal end of the papilla for the insertion has been considered the power arm; the length of the bone from proximal articular surface to the end of metatarsal three is the weight arm. The following are the ratios of power arm to weight arm expressed as per cent.

*Nesochen* and *Branta c. minima* with their shorter power arms are more efficient for speedy tarsal flexion. Whereas in respect to biceps femoris leverage the two species of *Branta* are alike (as noted above, p. 29), in respect to

TABLE 3  
LENGTH OF POWER ARM IN ACTION OF TIBIALIS ANTICUS

| Species                            | Number of specimens | Per cent power arm of weight arm |           |
|------------------------------------|---------------------|----------------------------------|-----------|
|                                    |                     | Average                          | Extremes  |
| <i>Nesochen sandvicensis</i> ..... | 4                   | 18.3                             | 17.7-18.9 |
| <i>Branta c. minima</i> .....      | 6                   | 18.6                             | 18.2-19.4 |
| <i>Branta nigricans</i> .....      | 6                   | 19.5                             | 19.0-20.1 |
| <i>Philacte canagica</i> .....     | 3                   | 19.9                             | 19.0-21.5 |
| <i>Anser albifrons</i> .....       | 8                   | 20.8                             | 19.3-22.4 |
| <i>Chen hyperborea</i> .....       | 5                   | 20.2                             | 19.6-20.6 |

tibialis anticus leverage they are different; *nigricans* is 5 per cent (average) more powerful per unit force of contraction and conversely *minima* is to the same degree quicker in its movement. The lever arm ratios for tarsal flexion vary more individually than do the ratios for the action of the biceps, yet the average differences must have significance. *Anser* is again at the opposite extreme of power efficiency from *Nesochen*. The advantage of power in the recovery stroke of the foot in the water and that of speed when the foot is used in running on land point to the adaptive value of these variations in leverage.

Leverage is not to be considered apart from bulk. In figure 9 it is seen that in *Nesochen* the loss of power efficiency is compensated for by greater bulk of muscle (about 20 per cent). Part of this superiority in bulk may serve for greater range of action, although it is not evident that the fleshy part in *Nesochen* was disproportionately longer than it was in the other forms. Greater bulk also is needed to overcome the weight drag of the relatively slightly heavier tarsometatarsus and toes. *Branta c. minima* has much less compensation for its loss of power in leverage; but, in this species the foot and tarsometatarsus are lighter than in *Nesochen*. *Chen* does not require a compensation for its leverage; its relatively heavy foot could account for the moderately large tibialis anticus. Both leverage and weight of foot and opposing musculature are factors in the mechanical equation that demands a given bulk development of the muscle.

The M. gastrocnemius is the largest of all the leg muscles. It is chiefly an extensor of the tarsometatarsus, which is a power movement of great importance in swimming, running, and climbing. The functions of the two major

divisions of the muscle must be considered separately. The first division, the external head, arises on the femur and exerts a force contributing to tibial flexion. Thus by causing both tibial flexion and tarsal extension it performs the essential movements of swimming. In running, however, tibial flexion would not be desirable and would have to be held in check by muscles such as the *M. extensor femoris*. The second division, the tibial head, is solely an extensor of the tarsometatarsus and has no connection with the femur. While it is useful in the tarsal movements of swimming, it is most efficient in running because it does not cause tibial flexion.

The small medial head is of slight importance in major power movements. By its attachment to the internal condyle of the femur it opposes to some degree a rotating action brought about by the attachment of the external head on the external condyle. It is probable that the medial head was primitively of comparable importance to the external head, both of which arise from the femur. The medial head has since been overshadowed as the principal medial division by the closely adjacent tibial head which probably has arisen from it, but which has developed attachments on the tibiotarsus only.

The total bulk of all divisions of the gastrocnemius displays variations which extend little beyond the range of individual variation in *Nesochen*. The muscle is important in all types of limb action and so is not disproportionately enlarged in any of the forms. The relative development of external and tibial head is significant. The external head expressed as percentage of tibial head is as follows: *Nesochen*, 56–59 (63, average of 3); *Branta c. minima*, 84; *Branta nigricans*, 102; *Philacte canagica*, 75; *Anser albifrons*, 91; *Chen hyperborea*, 85. *Anser* and *Branta nigricans* accord with expectations and show relatively great development of the external head, the last-named being the only one in which the external head surpasses the tibial head in size. *Philacte* displays a surprisingly small percentage. Although paralleling *Branta nigricans* in many points of aquatic adaptation, *Philacte* distinctly fails to conform in this particular.

The leverage gained by the *M. gastrocnemius* in tarsal extension is dependent upon the height of the hypotarsal ridges. A measurement was taken from the summit of the inner ridge to the point of the crest adjacent and internal to the internal cotyla, which point is opposite the center of the articulating surface of the cotyla. The measurement may be considered the power arm of the lever. The weight arm was the measurement of tarsal length as used previously for the *tibialis anticus*. (For power-arm values see table 4.)

Four stages in differentiation may be distinguished on the basis of the calculations of leverage. *Nesochen* is clearly the most adapted for speedy tarsal extension (running); *Branta c. minima* develops 5.2 per cent (average) more force and less speed; *Branta nigricans*, and *Chen*, 12–14 per cent more force; and *Philacte* and *Anser*, 19–20 per cent more force than *Nesochen*. Differences in the species in leverage gained by this muscle are greater than those for any of the other muscles analyzed. The relative positions of the species are not greatly altered with regard to adaptation for swimming and run-

ning. In the leverage of biceps and tibialis anticus actions, *Chen*, *Philacte*, and *Branta nigricans* are similarly grouped, while *Nesochen* stands at one extreme with *Anser* at the other. *Branta c. minima* in leverage of one muscle action is close to *Nesochen* (tibialis anticus), in another it is grouped with *B. nigricans* (biceps femoris) and in leverage of the action of the muscle just discussed (gastrocnemius) it is intermediate between *Nesochen* and *Branta nigricans*.

It should be emphasized that in *Nesochen* there is no compensation for loss of power in leverage by greater bulk out of proportion to the rest of the leg. The gastrocnemius of *Nesochen* is of course much greater in proportion to body weight than it is in *Branta nigricans*, and in this way overcomes loss of leverage.

*Muscle moving tarsometatarsus; one-joint group from tibiotarsus to tarso-metatarsus.*—The M. tibialis posticus, an accessory to the gastrocnemius as a

TABLE 4  
LENGTH OF POWER ARM IN ACTION OF GASTROCNEMIUS

| Species                            | Number of specimens | Average | Extremes  |
|------------------------------------|---------------------|---------|-----------|
| <i>Nesochen sandvicensis</i> ..... | 4                   | 13.55   | 13.2-13.8 |
| <i>Branta c. minima</i> .....      | 6                   | 14.25   | 13.8-14.6 |
| <i>Branta nigricans</i> .....      | 6                   | 15.15   | 14.7-15.9 |
| <i>Philacte canagica</i> .....     | 3                   | 16.23   | 15.8-16.8 |
| <i>Anser albifrons</i> .....       | 8                   | 16.36   | 15.7-16.9 |
| <i>Chen hyperborea</i> .....       | 7                   | 15.53   | 14.7-16.0 |

tarsal extensor, acts on the lateral surface of the tarsometatarsus. It is extremely weak but its strong tendon suggests that it may serve as a brace, possibly preventing a rotation of the tarsometatarsus that might otherwise result from the gastrocnemius acting, preponderantly, on the medial side of the hypotarsus.

*M. popliteus.*—This muscle serves to pull the free end of the fibula toward the head of the tibia. Evidently it is a brace against the action of other muscles attaching to the fibula that might cause the fibula to be pulled from its position beside the tibia.

*Two-joint toe flexors and tarsal extensors.*—The M. flexor perforatus indicus primus pedis and the M. flexor perforatus medius primus pedis are similar in their actions on the digits with which they connect. At their origins both make connections with the popliteal area of the femur and with the ambiens tendon. The interactions of the toe flexors and the ambiens have already been discussed (see p. 27).

These two flexors serve to flex the toes as a whole, working near the bases of the digits. The medius primus, besides flexing the third (middle) toe as a unit from the region of the first joint of the digit, also causes the second phalanx to bend on the first and so curves the toe. This action is brought about by the vinculum to the medius secundus tendon that runs to the second joint of the digit. Curvature of the toe probably does not result to so great a degree as



that induced by a direct pull on the medius secundus tendon by its own muscle. The indicus primus, attaching to the base of the second toe at the joint with the metatarsal, has a much less powerful leverage when the toe has become partly flexed than has the medius primus; it can in no way bend the second phalanx upon the first. The medial branch of the tendon of the indicus primus, present in *Nesochen* but lacking or weakly manifested in the others, appears to add strength and balance to the attachment.

Since the tendons of these flexors run over the heel, they also extend the tarsometatarsus, especially if toe flexion is opposed. When the tarsometatarsus is flexed, the tension in the tendons automatically flexes the toes. All the toe flexors of *Nesochen* have relatively long bellies. This was especially noticeable in the indicus primus (see p. 16) and in the M. flexor hallucis longus (see fig. 5). This length not only permits greater range of action associated with the partial freedom of the toes from the web, but, in running, allows the toes to be extended earlier in the recovery stroke. It will be recalled that an observed feature of the gait of *Nesochen* was the swinging forward of the foot with toes well extended. The advantage of *Nesochen's* power to hold the toes extended in the recovery stroke should be appreciable in running and climbing up a slope. A swimming goose or one running on smooth level ground has no need to prevent the automatic toe flexion when the foot is in forward progress. In swimming, such a flexion is needed to bring the web of the foot into the correct angle to thrust against the water in the initial phase of the swimming stroke.

Differences in the separation of the heads of the medius primus are pronounced (see p. 16). The functional significance of the complete separation in *Nesochen* would seem to be that a somewhat wider range and control of middle toe movements are possible. Because of this separation, contraction of the medial head is unhindered by fusion with the tibial head which has a shorter range of action.

The M. flexor perforatus annularis primus pedis combines the actions of the primus and secundus flexors in that it attaches to the first, second, and third joints of the fourth digit to effect both toe flexion and curvature. There can be no simple flexion from the base without curvature, except as the M. extensor digitorum longus might oppose curvature without completely checking basal flexion. When the bird is standing or running (propulsive stroke), curvature is of course prevented and the contraction of the flexors of the secundus group is effective in flexion of the entire digit. The annularis has the same influence upon tibial flexion and tarsal extension as other members of the primus group.

The M. flexor perforatus indicus secundus pedis, because of its origin on the femur, unbalanced by any ambiens attachment, must contribute slightly to tibial flexion in the same fashion as does the gastrocnemius. Since the insertion is on the first joint of the second digit, it can produce no more curvature than can the medius primus acting without its vinculum. Its action is flexion without curvature, although structurally it is classed with the secundus group.

The *M. flexor perforatus medius secundus pedis* is not attached directly to the femur and so brings about only tarsal extension besides its digital functions. The variable relations among the species with regard to the ambiens connection seem to have little functional significance. The *medius secundus* acts on the third digit to curve it at the first joint by pulling at the end of the second phalanx or region of the second joint (see comments on *medius primus*). By means of this muscle, toe curvature should be possible without flexion from the base, although the pull against the *medius primus* tendon which it perforates would tend to cause a slight flexion of the entire digit.

The *M. flexor longus hallucis* and the *M. flexor perforans digitorum profundus* function as a unit. For, although the former supplies a small tendinal division to the first digit, its subsequent junction with the tendon of the latter makes its function chiefly that of curvature of the three major toes through attachments to the ungual phalanges. As with the other flexors that attach distal to the first digital joints, these muscles act to cause flexion of the toe from the base when the foot is on the ground and bearing the weight of the bird. Even so, they would tend to thrust the claws downward into the ground. When free from the ground, these muscles can cause curvature without any great degree of accompanying basal flexion.

Bulk comparisons of all the toe flexors mentioned above have not yielded particularly significant differences. The only correlation clearly shown is that of bulk with size of toes. Throughout these muscles, *Branta nigricans* usually has greater relative bulk than *Branta c. minima*. The large-footed *Nesochen* and heavy, though short-footed, *Chen* are usually high in muscle bulk. One might expect the muscles that are important in cupping the web of the foot to be better developed in the swimming geese, but this is not so. Curvature is perhaps partly maintained by the elasticity of the web. The muscles of the distal phalanges are called upon importantly in *Nesochen* in climbing. This may offset lack of use in swimming.

The *M. soleus* and *M. peroneus longus* are intimately associated with the toe flexors but in action are principally tarsal extensors. The soleus is a weak extensor connecting to the tarsometatarsus indirectly by means of the ligamentous and cartilaginous sheaths that lie in the intercondylar sulcus and that tie into the proximal border of the tarsometatarsus. The *peroneus longus* causes both tarsal extension and flexion of the third digit. The extensor action seems the more important. Action upon the toe is through the junction of one of its divisions with the tendon of the *M. flexor perforatus medius primus pedis*. Possibly by means of the unusual position of the *peroneus* tendons in which they straddle the posterolateral surface of the heel joint, this muscle can balance even more than the *tibialis posticus* can balance the extensor action of the *gastrocnemius* which concentrates its force chiefly on the medial side of the hypotarsus and which may contribute to toeing-in. In view of this apparent function it is understandable that there is greater bulk in *Nesochen*.

*Two-joint toe extensor and tarsal flexor.*—The *M. extensor longus digitorum* functions as a toe extensor and, if opposed by the toe flexors, as a tarsal flexor.

This is the fourth unit of an interacting group of muscles. Intricate balance in tonus and contraction among the members accounts for various degrees of tarsal flexion and extension combined with toe flexion and extension. The four are the gastrocnemius, the tibialis anticus, the long toe flexors, and the extensor longus digitorum. Synergist action, the tendon effect, and the relaxation of tonus are important factors in the operation of this group.

The extensor longus digitorum is least developed in *Nesochen*. It appears probable that freedom of the distal phalanges from the web might ease the load on this muscle and explain the lesser bulk. Although this extensor does not connect as a direct tendon to the distal phalanges, the indirect connections by fasciae seem capable of extending the distal elements and opposing toe curvature.

*Short (one-joint) toe extensors and abductors.*—Extension and abduction is the function of the M. extensor hallucis brevis, this being the only extensor of the hallux. The muscle is noticeably larger in those forms (*Nesochen*, *Anser*, and *Chen*) in which the hallux is relatively large. The ungual phalanx is straightened in relation to the first phalanx in addition to extension of the digit from the base.

The M. abductor digiti II and M. abductor digiti IV are abductors of their respective digits with no powers of extension. In abducting they spread the toes from their bases and have no influence upon the distal joints of the digits. They are largest in *Nesochen* where fully spread toes would give stability in running, especially over irregular ground. In swimming the web probably acts as a parachute to spread the toes without much muscular aid.

The extensor brevis digiti III is purely an extensor of the third digit, operating on the basal segment only. It makes possible toe extension without the complication of tarsal flexion as obtains in the M. extensor longus digitorum. It is of functional significance only in *Nesochen* as it is little more than a tendon in the other forms.

*Short (one-joint) toe flexors and adductors.*—The M. flexor hallucis brevis is insignificant functionally. The M. adductor digiti II is chiefly an adductor of the second digit; it is extremely weak. The M. extensor brevis digiti IV is likewise chiefly an adductor but is better developed than is its counterpart serving the second toe. Again, *Nesochen* is superior in the development of these two short toe adductors. The toe adductors as a group are far less important functionally than the abductors because the tendons of the long toe flexors seem to be arranged so that they bring about some adduction when they flex. The extensor longus digitorum, on the other hand, cannot effect abduction.

#### AGE VARIATIONS IN *Nesochen*

The graph (fig. 10) shows that the one-year-old and six-year-old birds are much more similar, one to the other than to the juvenile. Among the large muscles therein represented, three are significantly different in relative size, namely, the M. extensor femoris, the M. semitendinosus, and the tibial head of the M. gastrocnemius. The muscles of the juvenile present noticeably greater extremes. This suggests less balance between muscle groups at this stage in

ontogeny. It is to be noted further that the especially large muscles of the juvenile are those involved in the power movements of running.

In the three muscles in which relative bulk in the juvenile departs distinctly from that of the others, the departures are not in the direction that makes the juvenile resemble adults of other geese. On the contrary, the direction is such that the juvenile resembles adults of other forms less than do the adults of

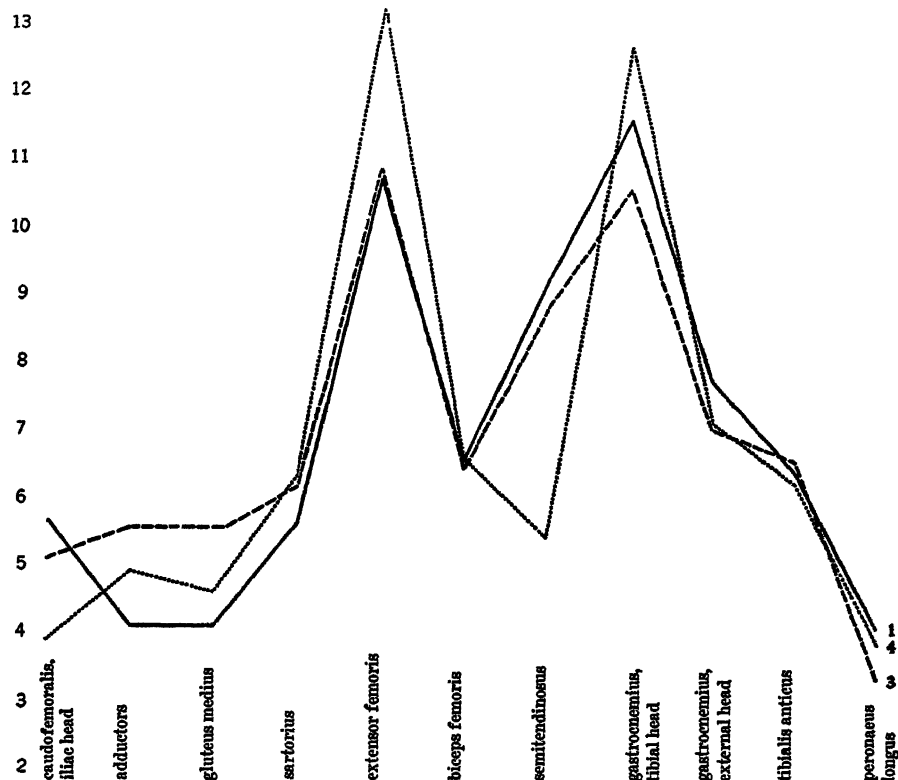


Fig. 10. Graph showing relative development of larger muscles of hind limb of *Nesoochen sandvicensis* in specimens of different age. Solid line, six-year-old bird (specimen no. 1); broken line, one-year-old bird (no. 3); dotted line, flightless juvenile (no. 4). Numbers at left indicate per cent of total leg muscle bulk.

*Nesoochen*. I do not interpret this as indicative of a phylogeny of the Hawaiian Goose leading back to an even more perfectly adapted land-dwelling type. The values of the levers and details of origins and insertions are closely similar to those of adults and would not bear out such a postulation. These differences in the bulk in the juvenile are to be regarded as necessary early adjustments to running (the power of flight was not yet developed). This is the young bird's only means of escape. Running power is attained by a rapid growth of the larger running muscles with a concomitant lag in the growth of some other muscles less vital at this period of life.

Bulks of the smaller muscles, under 4 per cent of the leg muscle bulk, have been compared and found to display no greater departures from the figures for the six-year-old bird than do those of the one-year-old.

## COMPARISON OF THE SKELETON

The skeletons of geese do not need redescription, for many of the elements have been well figured (Howard, 1929) and some have been studied carefully in connection with the identification of fossil species. There remain to be recorded here such differences in the forms with which I have dealt that seem to be fairly constantly present either as distinguishing features or as modifications that can be considered adaptive. Throughout the skeleton there are disappointingly few differences that are reliable in all instances even for use in separating the genera. For example, in the femur, where in some forms as many as eighteen examples have been available, features that seem potentially useful as generic characters break down in one or two members of a series. Actual size of any one element is in itself of little importance, since in *Branta*, *Chen*, and *Anser*, taking males and females together, a nearly continuous series of sizes may be found. However, ratios of sizes of one bone to another yield some significant differences as do also the ratios of length to width of a given element.

*Femur*.—*Branta* differs from *Chen* in that the medial crest bordering the popliteal area (attachment of the adductors) is less deflected medially and hence straighter and more in line with the shaft (pl. 1). The rotular groove is narrower in *Chen*, so appearing to be deeper. The outer surfaces of the condyles converge toward one another anteriorly in *Chen*, whereas they are more nearly parallel in *Branta* (pl. 1). In *Chen* the internal condyle is narrower. These features are usually reliable but are not perfectly constant as differentiating characters. Taken in combination, however, identity as to genus has been possible in all species studied. Muscle attachment scars, such as that of the *M. caudofemoralis*, and the course of the linea aspera of the shaft do not afford reliable characters.

*Anser* is closely similar to *Branta*. In the characters just described it is perhaps slightly closer to *Chen* than is *Branta*. All points considered it can usually be separated from *Chen* but not from *Branta*. *Branta c. minima* and *Branta nigricans* can be distinguished from *Anser albifrons* ssp. by their small size. They may be separated one from the other, if sex is known, by the smaller size of *nigricans* and by the less extensive popliteal excavation and the more deflected medial crest.

*Philacte* is similar to *Branta*, but in the two available specimens it displays a configuration of the popliteal area that is markedly different and which separates it from *Branta* as well as from all the other geese studied except *Chloëphaga*. This feature consists of a narrowing of the popliteal depression by inflation of the lateral margin so that the area takes the shape of a deep relatively narrow trough. *Chloëphaga* is identical in this respect. The femur of *Philacte* is stout and moderately short, although it overlaps the size range of *Chen h. hyperborea*.

*Nesochen* is not like any of the other genera in all respects. Size is equal to *Chen h. hyperborea* or to a small *Anser a. albifrons*. The medial border of the

popliteal area is equivalent to *Anser* and the condyles are parallel, but the rotular groove is extremely broad, more so than in any North American goose. The broad groove is associated with the large *M. extensor femoris* whose tendon occupies the groove. In this respect *Nesochen* is the antithesis of *Chen* and approaches *Chloëphaga leucoptera* wherein the groove is extremely broad. The resemblance to *Chloëphaga* is to be explained as a parallel modification, the result of land adaptation, and not necessarily an argument for close genetic relationship of *Nesochen* and *Chloëphaga*.

Still another feature of the femur of *Nesochen* is the short neck that curves less acutely medially (pl. 1). This configuration is highly suggestive of the Pliocene goose described as *Chen pressa* by Wetmore (1933, pp. 9-11). Wetmore uses the feature of short neck to separate *pressa* from the other species of *Chen*. The neck of *Nesochen* is not, however, so extremely shortened. Wetmore's illustrations show a broad rotular groove in *pressa* and his description reasserts this feature. Also the figure shows the condyles converging less anteriorly than in *Chen*. These last two points argue for relationships with *Branta* and *Anser* and especially *Nesochen* rather than with *Chen*. The border of the popliteal area is similar to *Chen*, however. Other features such as "the arrangement of the tubercles on the shaft" referred to by Wetmore I have found variable and they seem to me to be unsatisfactory for use in generic allocation. There is some doubt in my mind, then, as to the generic placement of the species *pressa*. There is rather more reason for placing it in the genus *Nesochen* than in *Chen*, though one may hesitate to associate it with a form now restricted to a peculiar insular habitat. Whether indicative of genetic relationships or not, the interesting fact remains that there are some important resemblances in the two forms. Broad rotular groove is a fairly certain sign of land adaptation. Although found in a lake deposit, *pressa* may have been an upland goose like certain species of *Chloëphaga* and like *Nesochen*.

*Tibiotarsus and fibula*.—The living North American genera are extremely similar with respect to this element. *Nesochen* is differentiated in several particulars, a few of which are constant in all individuals. *Nesochen* and *Branta c. minima* usually display a distal (anterior) margin of the inner cnemial crest more acutely deflected from the shaft than in the other species of *Branta* and the other genera. In *Nesochen* and *Branta c. minima* the cnemial spine of the inner crest usually projects more anteriorly and less proximally than in the others. The shaft is straighter both proximally near the head and distally near the condyles in *Nesochen*. The condyles are less offset medially. Further, the condyles in *Nesochen* are slightly smaller, more nearly equal, and the distal surfaces of them are less rounded posteriorly. The shaft in *Nesochen* is broader and less tapered in anterior aspect just proximal to the condyles (pl. 2). These modifications of shape of cnemial crest, of condyles, and of shaft are all factors in adaptation to nonaquatic life, serving to straighten the limb and to provide firm support.

By far the most readily observed characteristic of *Nesochen* is the relatively long fibular crest. The fibula itself is not larger in *Nesochen*, but if anything

smaller and no longer than in the others. Measurements of the crest reduced to percentages of tibial length average as follows: *Nesochen*, 20.5; *Branta c. minima*, 18.8; *Branta c. leucopareia*, 19.1; *Branta c. canadensis*, 17.8; *Branta nigricans*, 17.4; *Philacte*, 19.2; *Anser a. albifrons*, 18.4; *Chen. h. hyperborea*, 18.4; *Chen rossii*, 18.7. Only one individual, one of six *Chen h. hyperborea*, reaches the range in percentage of *Nesochen*. (For the differences in insertions of tibial flexors see pp. 10, 28, 29.)

The characteristics of *Nesochen* do not appear in *Chloëphaga*, except that the condyles are even more directly in line with the shaft in the latter. The fibular crest is distinctly short in *Chloëphaga*. In this connection should be mentioned *Branta dickeyi* of the Pleistocene of McKittrick, the type of which I have had for examination. Little can be added to the original description (L. Miller, 1924, p. 179-180), except that additional swan material bears out the distinction between geese (*Branta*) and swans in the matter of the degree to which the condyles are offset medially. Since I have not found characters to separate tibiotarsi of *Anser*, *Branta*, and *Chen* I cannot reaffirm the generic assignment. But, on the other hand, there is nothing to indicate that *dickeyi* was anything other than a *Branta*. *Branta* today contains the largest species of North American geese which approach most closely the giant *dickeyi*. One important character can be added to the description of *dickeyi*, namely, the long fibular crest which in the type is 21 per cent of the tibial length.

*Tarsometatarsus*.—Characters of this element present some significant resemblances and differences. Among *Branta*, *Chen*, and *Anser* no one character alone serves to separate the genera, but several in combination can be depended upon to effect a satisfactory identification. *Branta* displays an inflation of the lateral margin of the bone just distal to the head which is less pronounced in *Anser* and which usually is lacking in *Chen* (pl. 3). The trochlea of the second metatarsal joins the shaft of the bone at a more abrupt angle and is shorter in *Branta* than in the others, especially *Chen*. *Branta nigricans* is not typical of *Branta* in this respect.

In *Anser* the medial side of the hypotarsus makes a less acute angle with the remainder of the medial surface than in the other two, and the tendinal groove of the anterior surface is more prominent. The entire bone often is slightly more stocky. Measurements of width of proximal and distal ends and of the shaft, all in relation to length, show greater average dimensions in *Anser*, but it must be emphasized that there is a great amount of overlap in the figures for the different genera.

*Nesochen* resembles *Chen* and *Branta* in the shape of the medial surface of the hypotarsus and in the anterior tendinal groove; it resembles *Chen* in the matter of inflation of the lateral surface distal to the head and in the shape of the trochlea of the second metatarsal. The figures representing the relative breadth are close to those for *Branta* and *Chen*. The outer margin of the shaft is straighter than in any of the others, as a result of the thickness, distally, of the fourth metatarsal shaft. This gives an appearance of straightness and uniformity of shaft throughout its length, with trochleae directly in line with the

shaft. This latter feature is to be associated with running habits as is also the height of the metatarsal ridges and the insertion point of the *tibialis anticus* (pp. 32-35).

*Philacte* is markedly different from the genera just mentioned in the shape of the distal end. The plantar surface just proximal to the trochleae is much flatter and broader and the second metatarsal more sharply deflected medially (pl. 3). By actual measurement the distal end of the bone across the trochleae is about 5 per cent wider relative to the length of the bone than in

TABLE 5  
AVERAGE AND EXTREME VALUES FOR TOE LENGTH  
(in percentages)

| Species                                                               | Number of specimens | Digit 1                           | Digit 2          | Digit 4                           |
|-----------------------------------------------------------------------|---------------------|-----------------------------------|------------------|-----------------------------------|
| <i>Nesochen sandvicensis</i> . . .                                    | 3                   | 20.4 (18.9-22.4)                  | 77.0 (75.6-77.8) | 96.9 (94.8-98.5)                  |
| <i>Branta c. minima</i> . . . . .                                     | 5                   | 13.5 (12.7-14.6)<br>(3 specimens) | 77.0 (75.3-77.6) | 94.2 (93.8-94.6)<br>(4 specimens) |
| <i>Branta c. canadensis</i> and<br><i>Branta c. leucopareia</i> . . . | 4                   | 16.5 (16.0-17.1)<br>(2 specimens) | 76.9 (75.5-79.1) | 96.2 (95.3-97.1)                  |
| <i>Branta nigricans</i> . . . . .                                     | 6                   | 16.3 (14.5-16.9)<br>(4 specimens) | 77.6 (76.1-78.4) | 98.4 (97.2-101.0)                 |
| <i>Philacte canagica</i> . . . . .                                    | 2                   | 19.8 (19.5-20.2)                  | 74.9 (74.7-75.1) | 98.1 (98.1-98.2)                  |
| <i>Chloëphaga leucoptera</i> . . .                                    | 2                   | 22.1 (21.3-23.0)                  | 74.7 (74.7-74.8) | 95.6 (94.5-96.8)                  |
| <i>Anser a. albifrons</i> . . . . .                                   | 8                   | 18.6 (17.2-20.7)<br>(6 specimens) | 75.7 (73.4-77.2) | 96.8 (94.4-99.2)<br>(7 specimens) |
| <i>Chen h. hyperborea</i> . . . . .                                   | 6                   | 19.2 (18.1-20.7)<br>(4 specimens) | 74.3 (72.4-75.3) | 96.3 (93.9-98.7)                  |
| <i>Chen rossii</i> . . . . .                                          | 2                   | 18.5 (18.0-19.0)                  | 75.0 (74.8-75.2) | 94.0 (92.7-95.2)                  |

*Branta*, *Anser*, *Chen*, or *Nesochen*; but, the flattened appearance of the end is more striking than is the measurement. No close approach in shape occurs in any other North American geese or in *Nesochen*. Significantly, however, *Chloëphaga* is identical with *Philacte* in all major features of shape of the distal end.

The shape of the medial surface of the hypotarsus of *Philacte* is between *Anser* and *Branta*; in *Chloëphaga* it is even more sharply angled than in *Branta*. *Philacte* has a swollen lateral surface distal to the head as in *Branta* which may or may not be present in *Chloëphaga*. These latter features appear to be much less significant than the special configuration of the distal end common to *Philacte* and *Chloëphaga*.

*Digits*.—Points of difference having to do with the digits all pertain to relative lengths of the several digits and of phalanges comprising them. The digits were measured from the cleaned bones in articulated position, exclusive of the ungual phalanx. Measurements of the individual phalanges were taken as the greatest length, not as distance between articulating surfaces. The length of digit three was used as a standard of comparison and the measurements of the



other toes expressed in percentages of it. Average and extreme values for toe length in per cent are shown in table 5.

The most decisive differences are in the length of the hallux. *Branta* is set off from all the others without individual overlapping. The hallux of *Chloëphaga* is extremely long. Individual variation is greater in this vestigial digit than in the functional digits. Digit two is relatively short in *Chen*, *Philacte*, and *Chloëphaga*. *Anser* is intermediate. Differences in relative length of digit four are less pronounced. *Chen* and *Chloëphaga* have somewhat shorter fourth digits, but this digit is short also in *Branta canadensis* (all races). This digit is especially long in *B. nigricans* and *Philacte*, both maritime forms. All major digits of *Chen* were visibly stouter than those in *Branta*, *Anser*, and *Nesochen*.

To demonstrate certain differences in lengths of phalanges composing a digit, each measurement of phalangeal length has been reduced to percentage of the basal phalanx of the digit concerned. The average and extreme values for these phalanges in the same specimens listed in the preceding table are :

TABLE 6  
LENGTHS OF PHALANGES  
(in percentages)

| Species                                                         | Digit 2    | Digit 3    |            | Digit 4    |            |            |
|-----------------------------------------------------------------|------------|------------|------------|------------|------------|------------|
|                                                                 | Phalanx 2  | Phalanx 2  | Phalanx 3  | Phalanx 2  | Phalanx 3  | Phalanx 4  |
| <i>Nesochen sandvicensis</i> .                                  | 70 (69-71) | 66 (65-67) | 60 (59-61) | 64 (63-66) | 52 (51-53) | 56 (55-57) |
| <i>Branta c. minima</i> . . . . .                               | 70 (69-72) | 64 (63-66) | 52 (51-53) | 61 (59-63) | 46 (43-48) | 48 (47-49) |
| <i>Branta c. canadensis</i> and<br><i>Branta c. leucopareia</i> | 70 (65-74) | 66 (63-68) | 55 (51-57) | 65 (61-68) | 49 (47-52) | 52 (47-55) |
| <i>Branta nigricans</i> . . . . .                               | 74 (72-76) | 66 (63-69) | 54 (52-57) | 67 (66-68) | 51 (48-54) | 55 (54-57) |
| <i>Philacte canagica</i> . . . . .                              | 71 (69-74) | 68 (67-70) | 59 (57-61) | 65 (65-66) | 51 (50-53) | 57 (57-58) |
| <i>Chloëphaga leucoptera</i> .                                  | 64 (63-66) | 65 (64-66) | 51 (50-53) | 64 (same)  | 50 (49-52) | 50 (49-51) |
| <i>Anser a. albifrons</i> . . . . .                             | 71 (69-73) | 68 (66-70) | 57 (55-60) | 64 (63-66) | 48 (45-50) | 54 (48-60) |
| <i>Chen h. hyperborea</i> . . . .                               | 68 (67-70) | 64 (63-66) | 52 (50-55) | 60 (56-64) | 46 (44-50) | 48 (46-51) |
| <i>Chen rossii</i> . . . . .                                    | 66 (64-68) | 63 (same)  | 48 (48-49) | 57 (55-60) | 42 (42-43) | 42 (42-43) |

*Chen*, *Chloëphaga*, and *Branta c. minima* have the shortest distal phalanges. *Branta nigricans*, *Philacte*, and *Nesochen* usually have the longest distal segments. The subterminal phalanges (second phalanx of digit two, third of digit three, and fourth of digit four) display the greatest range of differentiation. Table 7 shows that *Chen* and *Chloëphaga* possess short toes (middle toe) in relation to the femur, that *Nesochen* possesses long toes, that in the genus *Branta*, *minima* possesses shorter toes than *nigricans*, and that *Chen rossii* possesses shorter toes than *Chen hyperborea*. It seems safe to conclude that, in general, elongation or shortening of the toe as a whole is accomplished by a greater change in the distal (subterminal) phalanges than in the more proximal ones. A gradient seems to exist in the series of phalanges, especially in digit four. Table 5 shows that *Philacte* has a short second digit but a long fourth; correspondingly, the distal phalanges of digit two are relatively short and

those of digit four long. In *Branta c. minima*, digit two is long and four is short; distal phalanges of two are at least average, those of digit four short.

When relative lengths of digits two and four are compared with middle toe length (in relation to femur), another significant principle is apparent, even though it may break down in a few comparisons. This is the principle that forms with short middle toe (relative to femur) have even shorter lateral toes. This is demonstrated in both species of *Chen*, in *Chloëphaga*, and in the fourth toe of *Branta c. minima*. Conversely, if the middle toe is long, the lateral toes are even longer. This is seen in *Nesochen* and *Philacte*; it holds true in *Branta nigricans* only when compared to *Branta c. minima* or when middle toe is compared to tarsometatarsus rather than to femur.

TABLE 7  
LENGTHS OF LIMB SEGMENTS IN PER CENT

| Species                                                               | Number of specimens | Tibiotarsus                    | Tarsometatarsus | Middle toe                  |
|-----------------------------------------------------------------------|---------------------|--------------------------------|-----------------|-----------------------------|
| <i>Nesochen sandvicensis</i> .....                                    | 4                   | 192 (189-195)                  | 117 (115-119)   | 95 (92-98)                  |
| <i>Branta c. minima</i> .....                                         | 5                   | 188 (185-190)<br>(4 specimens) | 112 (110-115)   | 78 (72-82)<br>(4 specimens) |
| <i>Branta c. canadensis</i> and<br><i>Branta c. leucopareia</i> ..... | 5                   | 184 (183-186)                  | 106 (102-109)   | 80 (76-85)<br>(4 specimens) |
| <i>Branta nigricans</i> .....                                         | 5                   | 182 (177-188)                  | 104 (102-107)   | 82 (78-87)                  |
| <i>Philacte canagica</i> .....                                        | 2                   | 169 (166-173)                  | 97 (94-101)     | 83 (82-84)                  |
| <i>Chloëphaga leucoptera</i> .....                                    | 2                   | 186 (181-191)                  | 109 (108-110)   | 74 (72-76)                  |
| <i>Anser a. albifrons</i> .....                                       | 7                   | 179 (176-186)                  | 103 (101-109)   | 89 (86-94)                  |
| <i>Chen h. hyperborea</i> .....                                       | 7                   | 187 (182-194)                  | 114 (110-117)   | 79 (74-86)                  |
| <i>Chen rossii</i> .....                                              | 2                   | 189 (185-194)                  | 113 (109-116)   | 73 (71-75)                  |

To summarize, increase or decrease in toe length takes place to a greater degree in digits two and four than in three, and increase or decrease in phalangeal length takes place to a greater degree in distal (exclusive of ungual) than in proximal phalanges. This would seem to be an instance of heterogonic growth in which the lateral digits and distal phalanges possess a faster growth rate than their central and basal counterparts. Hence, a change in the size of the foot region as a whole results in disproportionate changes in the parts in question. The hallux clearly is not a factor in these heterogonic relationships.

*Length of hind limb segments.*—Although *Nesochen* has a leg much larger than any of the other geese, the total length of it from acetabulum to subterminal phalanx of the middle toe is not outstandingly greater than in some of the others. Total length in *Nesochen* varies from 347 to 376 mm.; *Chen hyperborea*, a bird of similar size, varies from 332 to 373 mm. Legs of *Anser albifrons* vary from 327 to 359 mm., whereas the bird is much larger otherwise than *Nesochen*. *Branta nigricans* is short-legged relative to body size, but *Branta c. minima* is about as long-legged proportionately as *Nesochen*.

In the matter of length of the limb segments there are some important generic differences. Tibiotarsus, tarsometatarsus, and middle toe exclusive of ungual phalanx have each been divided by length of femur to show relative length (see fig. 11) ; average and extreme percentages are shown in table 7.

The tarsometatarsus and tibiotarsus are remarkably similar in relation to the femur. The swimming geese, *Branta nigricans*, *Philacte*, and *Anser* possess shorter tibiotarsi and tarsometatarsi, or, inversely, longer femora. Comparison within the genus *Branta* is especially instructive in the differentiation it shows among the races and species. The femur is, I believe, relatively stable phylogenetically and is little altered in relation to body bulk. *Chloëphaga* constitutes an exception (see p. 52) in which the femur is long relative to the pelvis and humerus. The longer-legged geese, *Nesochen*, *Branta c. minima*, *Chloëphaga*, and *Chen*, have attained length through elongation of the tibial and tarsal segments with or without lengthening of the toes.

The histogram (fig. 11c) representing length of the middle toe presents a decidedly different outline from the histograms showing tarsal and tibial length, demonstrating clearly that toe length and tarsal length are not correlated. *Chloëphaga*, *Branta c. minima*, and *Chen* are short-toed, although possessed of long tarsometatarsi and tibiotarsi. *Anser* is long-toed but short in tarsometatarsus and tibiotarsus. *Nesochen* is long in all three segments. The relations of tarsometatarsus and toes in the races of *Branta canadensis* bear out Grinnell, Bryant, and Storer's findings (1918, pp. 226-227) regarding tarsal proportion based on external measurements.

*Pelvis*:—Two features of the anterior part of the ilium of *Nesochen*, more particularly the tendency to rounded contour of the fossa and the more perpendicular surfaces, have already been noted (see p. 8). The length of the pelvis, measured from anterior end to posterior notch of ilium, corresponds roughly to the length of the femur. In the relation between femur and pelvis there is some individual variation, the femur varying from 51 to 62 per cent of pelvic length in *Branta*, for example, with no decisive specific differences. *Nesochen* does not exceed the upper range of variation in *Branta*, but the four examples average 60 per cent while nineteen specimens of *Branta* average 58. *Chen* and *Anser* average 57 and 58, respectively (12 specimens of each). Three specimens of *Philacte* average 62 and two of *Chloëphaga* figure 66 and 69. *Chloëphaga* is outstanding, then, in possessing a relatively long femur, or conversely, short pelvis. *Philacte* shows similar tendencies and *Nesochen* varies from the others in the same direction.

Great length of postacetabular region compared to pre-acetabular region is regarded as a mark of aquatic adaptation. *Branta*, *Philacte*, *Anser*, and *Chen* are extremely uniform in this regard, but in *Nesochen* the postacetabular length relative to total length of pelvis is about 4 per cent less, and in *Chloëphaga* 12 per cent less, than in the others. Large size and more powerful leverage of the *M. biceps femoris* and *M. semitendinosus* in swimming types is to be associated with great postacetabular length. The low figure for *Chloëphaga* might be regarded as showing a lack of aquatic adaptation, but since

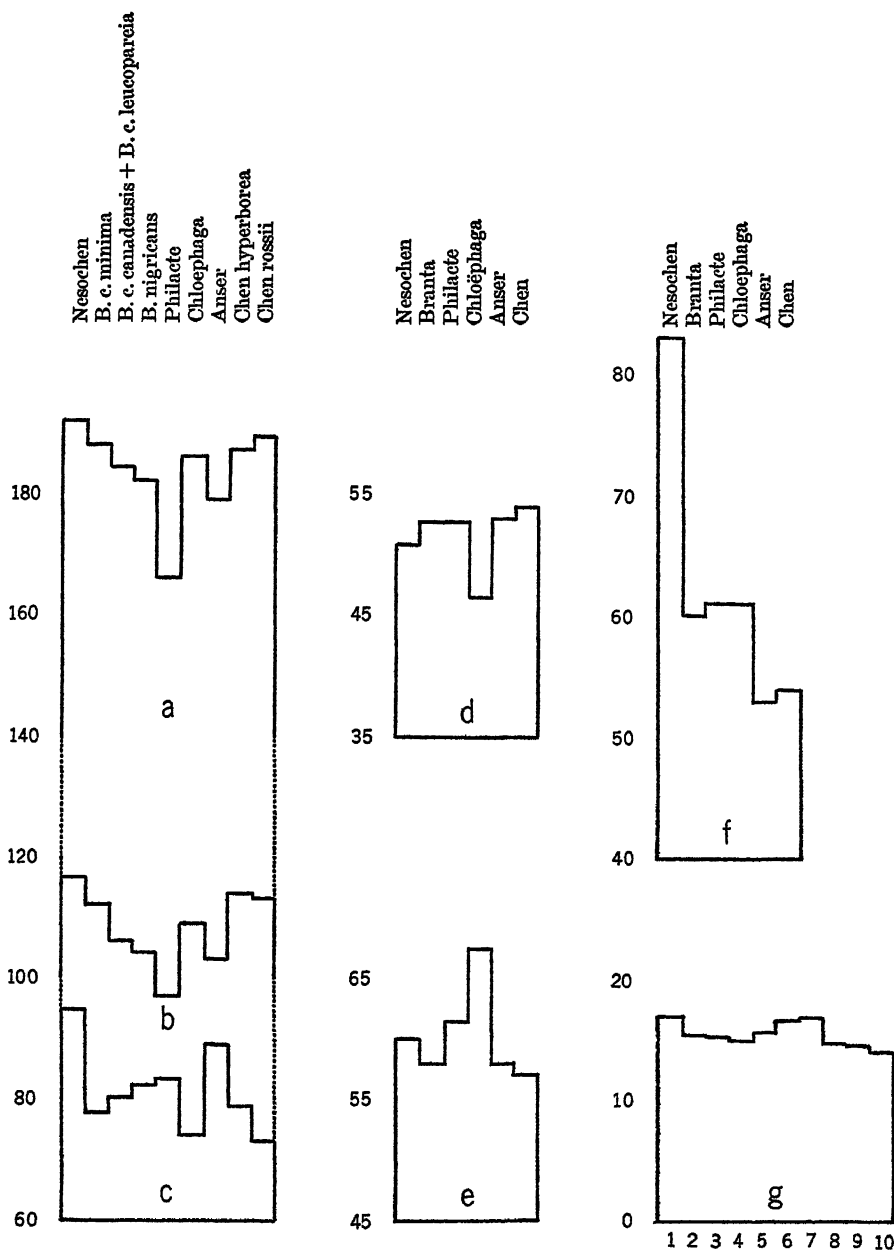


Fig. 11. Histograms showing relative sizes and proportions of skeletal parts in different kinds of geese.

a, b, and c show lengths of hind limb segments as per cent of femoral length. a, tibiotarsus; b, tarsometatarsus; c, middle toe without ungual phalanx.

d, postacetabular pelvic length as per cent of total pelvic length.

e, length of femur as per cent of total pelvic length.

f, extent of ilio-ischiatic fenestra as per cent of postacetabular length of pelvis.

g, depth of pelvis at acetabulum as per cent of total pelvic length. 1. *Nesochen*; 2. *B. c. minima*; 3. *B. c. leucoparctica*; 4. *B. c. canadensis*; 5. *B. nigricans*; 6. *Philaete*; 7. *Chloephaga leucoptera*; 8. *Anser albifrons*; 9. *Chen hyperborea*; 10. *Chen rossii*.

other parts of the limb structure do not show this lack to such a marked degree, I doubt whether nonaquatic adaptation is the sole explanation in this instance.

The depth of the pelvis is visibly greater in *Nesochen*, *Chloëphaga*, and *Philacte*, and averages greater in some of the species of *Branta* than in *Chen* and *Anser*. The depth at the acetabulum from dorsal surface to the obturator foramen calculated as percentage of pelvic length serves to express this difference quantitatively. Averages with extremes follow: *Nesochen*, 17.0 (three the same); *Branta c. minima*, 15.5 (15-17); *B. c. leucopareia*, 15.5 (15-16); *B. c. canadensis*, 15.0 (14-16); *Branta nigricans*, 15.8 (15-17); *Philacte*, 16.7 (16-17); *Chloëphaga*, 17.0 (two the same); *Anser albifrons*, 14.8 (14-16); *Chen hyperborea*, 14.7 (14-16); *Chen rossii*, 14.2 (14-15).

Comparison of figures 11e and 11g demonstrates that the same forms that have short pelves (long femora) have the deepest pelves. This indicates that variation is one of length of pelvis with depth and femoral length fairly constant. Nevertheless, the appearance of the inflated ilium above the acetabulum in *Nesochen* suggests that the pelvis has become especially deep and massive for the origins of the limb muscles. Lesser depth in *Chen* and *Anser* than in *Branta* is apparent; all three bear the same ratio of femoral to pelvic length.

The posterior extent of the ilio-ischiatic fenestra is strikingly large in *Nesochen* (pl. 2f). Length of fenestra from acetabulum has been reduced to percentage of postacetabular length. Averages and extremes are: *Nesochen*, 83 (82-83); *Branta*, 60 (50-71); *Philacte*, 61 (57-67); *Chloëphaga*, 61 (54-69); *Anser*, 53 (41-62); *Chen*, 54 (38-65). Twenty-one specimens of *Branta*, thirteen of *Anser*, and eleven of *Chen* were available; the four examples of *Nesochen* were extremely uniform; two specimens of *Chloëphaga* and three of *Philacte* were at hand.

The only muscles connected with the posterior part of the ilio-ischiatic fenestra are the M. obturator externus and the iliac head of the M. caudofemoralis. The first muscle does not occupy the posterior part of the fossa but is connected to the posterior border by fascia. The second does have a greater posterior extension in *Nesochen* corresponding to the large fenestra, which extension is interpreted as useful in effecting greater range of femoral extension. The muscle was not found to be different in bulk compared with other genera. It attaches on flat bone surfaces, on surface fascia, and on the margins of the fenestra. If the margins of the fenestra were strengthened to provide strong attachments, one could account for the size of the opening as being a necessary concomitant of posterior extension of the muscle. But, the margins are weak and only slightly stronger than the fascia of the fenestra; their nature does not suggest a functional explanation for its large size. I am inclined, therefore, to view this feature as nonadaptive, but highly characteristic of the genus *Nesochen*.

Numbers of vertebrae were counted in all the sacra examined and found to vary from 17 to 20. Undoubtedly age has something to do with fusion of caudal vertebrae to the sacral complex. Constant differences in species and genera do not exist. The minimum number occurred only in *Chen rossii*,

*Branta nigricans*, *B. canadensis*, and *Chloephaga leucoptera*, both specimens of the latter having only 17 fused vertebrae.

*Sternum*.—The sternum, like the pelvis, is subject to a wide range of individual variation in shape. It clearly may be seen that *Nesochen* has a smaller sternum than have other geese of comparable size. This is not manifested, however, in the length of the structure. Length was compared to length of pelvis; the ratio between the two proved to be highly variable individually so that

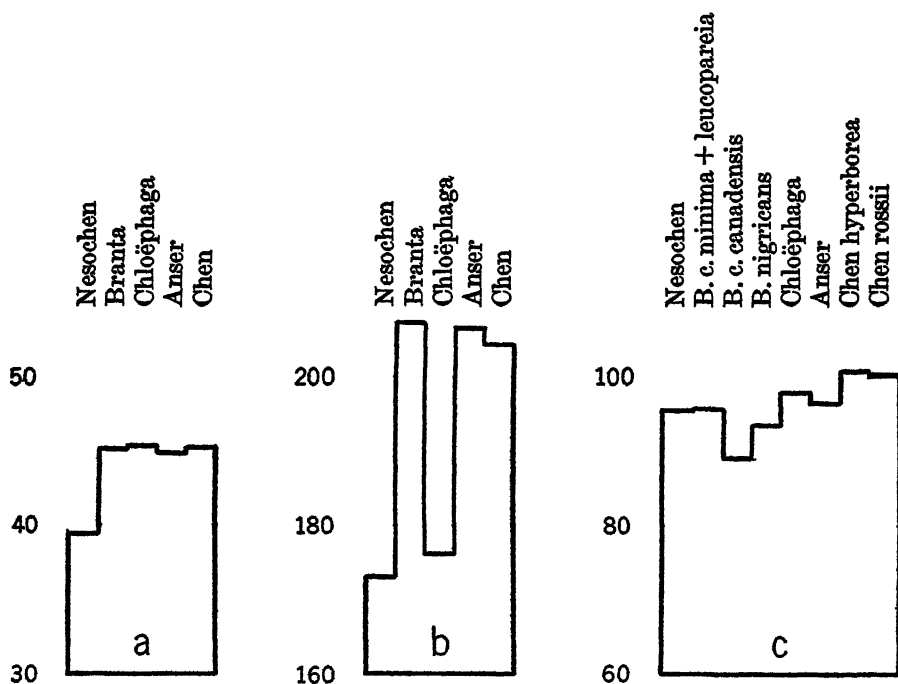


Fig. 12. Histograms showing relative sizes and proportions of skeletal parts in different kinds of geese.

a, width of sternum across costal facets as per cent of sternal length.

b, length of humerus as per cent of femoral length.

c, length of ulna as per cent of humeral length.

no generic differences could be detected. In the matter of width of sternum (narrowest point across costal facets), relative to length, *Nesochen* is importantly differentiated from all others. In the others the width averages 45 per cent of sternal length (minimum 42 per cent), the several genera varying from one another only fractionally in this relationship. The sterna of *Nesochen* were 39 and 40 per cent. This narrowness of course means lesser areas for attachments of the pectoral muscles and is one of a number of indices of the reduction in power of flight.

The carina is visibly lower in *Nesochen* than in the others. It is difficult to measure this difference accurately because the carinal apex is of nearly equal height in all the geese. The differences in height are manifested only posteriorly where no fixed points for measurements can be selected.

Dorsal and ventral manubrial spines in many particulars are inconstant in shape. The ventral spine is especially weak in *Nesochen* (pl. 4e). In *Branta*, *Philacte*, and *Anser* the dorsal spine is a simple dorsally projecting, button-like elevation. In *Chen* it is usually the same, but in some individuals and in *Chloëphaga* it is partly divided medially by an anterior and ventral groove. In *Nesochen* the dorsal spine is distinctly different, taking the form of a transverse elevated ridge, less thick than the buttonlike prominence of the others but two or three times as wide.

The pneumatic foramen in *Branta*, *Anser*, *Philacte*, *Chloëphaga*, and *Chen* is a large opening 3 to 5 mm. across, except in two specimens of *Anser albifrons gambelli* wherein the foramen is obstructed by an abnormal ridge of bone in this region. In *Nesochen* the foramen is almost closed, being less than a millimeter wide.

Three features characterize the sternum of *Chloëphaga*. First, the long posterolateral processes project especially far beyond the xiphial area. Second, the sternocoracoidal process is longer and projects farther anteriorly than in other geese. Third and perhaps most importantly, the surface posterior to the dorsal lip of the coracoidal sulcus is flattened, not deeply concave as in others.

*Coracoid*.—This element does not vary significantly in size relative to the sternum. The sternum is, however, so unstable individually that differences that might exist in coracoidal size may be obscured by using the sternum as an object of reference. Although not expressible numerically, the coracoid of *Nesochen* is smaller proportionately than in all the other geese. For example, it is about the size of that of *Philacte*, *Branta nigricans*, and *Branta c. minima*, although in weight these species are 200 to 400 grams lighter. In the island bird coracoidal length does not exceed 56 mm. which is a full centimeter shorter than the smallest coracoid of *Chen h. hyperborea*, a species of comparable weight. The bone would appear to average longer in *Chen* and especially in *Chloëphaga* than in *Anser* and *Branta*. Compared to the humerus the coracoid is longer in *Chloëphaga* than in others.

The length of the sternal facet was not found to differ significantly, but width of the anterior end differs somewhat. The latter is narrowest in *Nesochen*, not because of a reduction of the shaft but because of a noticeable reduction of the procoracoid and the brachial tuberosity (pl. 5). The depression between the procoracoid and the brachial tuberosity is shallow. These features are indicative of weaker ligamentous and muscular attachments that go with lesser powers of flight. Other features of *Nesochen* are the angle of the coracohumeral surface, which surface tends to become more transverse to the shaft, and the greatly reduced pneumatic foramina below the brachial tuberosity. These foramina vary extensively in pattern but are always present except in *Chloëphaga*. In *Nesochen* they are reduced to one or two apertures less than 1 mm. across. There is only one differential character in *Branta*, *Anser*, and *Chen*. In *Branta* a greater dorsal overhang of the medial ventral edge of the brachial tuberosity occurs. Associated with this, it is found that pneumatic

foramina rarely occur in this medial region in *Anser* and *Chen* but often are present beneath the overhang in *Branta*.

Another important feature of *Nesochen* is the straight intermuscular line on the ventral surface of the shaft which is bowed laterally in *Branta*, *Philacte*, *Anser*, and *Chen*; in *Chloëphaga* the line is greatly altered so that it reaches to the lateral surface of the shaft at one point (see pl. 5a-e). On the sternum of *Chloëphaga* the intermuscular line bounding the outer margin of the *M. pectoralis secundus* correspondingly is deflected laterally.

Entirely comparable differences in the intermuscular line of the coracoid have been noted in the cormorants by Lambrecht (1931, pp. 79-81) and the conclusion reached that a shift of the line medially meant increase in size of the *M. pectoralis tertius* (coracobrachialis posticus) at the expense of the *M. pectoralis secundus* (supracoracoideus). This means in turn the reduction of flight power; an opposite shift in the line means an increase in power. I do not doubt that the relative developments of these muscles denote these differences in flight because in many living birds there is a positive correlation between flight and position of the line. The mechanical explanation of it that has been offered is not to me entirely satisfactory, however. There is no question about the function of the *pectoralis secundus* in flight. It serves to lift the extended wing and rotates the humerus so that the deltoid crest is moved dorsally. The contraction of the muscle is an important element in flight and reduction of it would indicate weakness in the control and use of the wing.

The precise action of the *pectoralis tertius* is in doubt. Lambrecht (*loc. cit.*) quoting Precht suggests that it serves only when the wing is extended from the body or when spread in the downward stroke, but he does not state its exact action at such times. Shufeldt (1890, p. 76) says that in the raven the muscle assists the *pectoralis secundus* in elevating the humerus, but I fail to see how it could so act, although it tends to rotate the deltoid crest upward by depressing the ulnar border. In this respect it is similar in action to the *secundus* but it can not lift the humerus as does the latter. Burt (1930, p. 485) speaks of the *tertius* pulling the humerus downward in opposition to the *secundus*. This is true, but in this connection it seems to be important that, while pulling the humerus down and back, the *tertius* rotates the bone into the position the humerus normally takes when the wing is folded. The *pectoralis major* likewise pulls the humerus down but rotates it so as to bring the flight surface into the horizontal in opposition to the action of the *tertius*. Regardless of how the *tertius* may serve as an auxiliary or brace in flight movements, it does not contribute importantly to the power of the action. Instead, it seems important in holding the humerus with ulnar crest depressed in the customary folded position of the wing. It should, therefore, at least not diminish, and perhaps would increase, in a species making little use of its wings for flight.

*Scapula and furcula*.—In *Nesochen* they are proportionately somewhat smaller than in other geese and the processes are weaker.

*Humerus*.—No reliable differences were discovered in the configuration of the distal end. On the proximal end the differences in the depression for the



external margin of the *M. triceps* are important. Wetmore (1924, p. 7), evidently referring to this depression, says that the sea geese or brant differ from the *Branta canadensis* group "in that they lack the impressed space on the head of the shaft below the caput humeri, a character in which brant resemble *Chen* and *Anser*." This depression, when pronounced, seems to me to indicate greater strength of triceps attachment and probably greater power of action. The differences between species is, in general, that indicated by Wetmore, but the differences are not as constant as might be desired. *Chen*, *Anser*, *Philacte*, or *Nesochen* have no more than a trace of this depression. *Branta nigricans* can be distinguished from these by the fact that the depressed area, though no deeper, is more abruptly set off from the head proximally. Three examples of *Branta c. minima* are indistinguishable from *nigricans*, whereas six others have a deeper depression such as Wetmore ascribes to the *canadensis* group. One *B. c. canadensis* has a very faint impression. Wetmore's fossil *B. minuscula* has a distinct impression. In *Nesochen* the impression is almost lacking, but in its proximal and lateral extension it resembles *Branta* slightly more than it does *Anser* or *Chen*.

*Chloëphaga* presents the most striking modification. In this genus the depression is much greater and broader than in *Branta*, extending far laterally and proximally so that it is overhung by the crest of the head. Correlated with the lateral extension of the depression is the straighter ridge of the shaft on the anconal surface just distal to the head in *Chloëphaga*, *Branta*, and *Nesochen*. Aside from these features I am unable to characterize separately *Branta*, *Philacte*, *Anser*, and *Chen*, and cannot discover any characters to separate the last-named three, one from another.

*Chloëphaga* is further set off from the North American geese by the breadth of the head which compared with humeral length averages about 10 per cent greater. This breadth in *Chloëphaga* is largely the result of an external flaring of the deltoid crest. In *Nesochen* the head is not relatively narrower than in the North American geese but the deltoid crest is less curved and is weaker throughout. The pneumatic foramen tends to be more restricted and the shaft is straighter distally than in all other geese examined. The middle of the shaft is curved as much as in the others. *Chloëphaga* and *Branta* display the extreme of curvature distally. Evidently, with the type of flight indulged in by geese, curvature of the shaft indicates strength of flight. It appears to be correlated with depth of the triceps impression and development of deltoid crest. Variations in width of the distal end were found to be insignificant.

The length of the humerus has been compared with that of the femur. In per cent of femoral length the genera average as follows: *Nesochen*, 173; *Branta c. canadensis* and *B. c. leucopareia*, 211; *Branta c. minima*, 204; *Branta nigricans*, 204; *Chloëphaga*, 176; *Anser*, 206; *Chen*, 204. I believe that *Nesochen* and *Chloëphaga* are short for different reasons. In the comparison of the femur with the pelvis it was found that the femur in *Chloëphaga* was exceptionally long (17 per cent greater than in *Anser* and *Branta*). The leg as a whole was not especially long as in *Nesochen*. Therefore in comparing hu-

merus with femur in *Chloëphaga* the low figure (15 per cent less than in *Anser* and *Branta*) does not mean relatively short wing. The femur, although usually to be considered a conservative element reflecting the body size with some accuracy, is unquestionably a relatively long bone in *Chloëphaga*. A single skeleton of *Philacte* shows a decided approach to *Chloëphaga* in the matter of long femur and relatively short humerus. In *Nesochen* the femur is but slightly longer relative to the pelvis than in *Branta*, *Chen*, and *Anser* and, of course, in relation to distal segments of the leg is short, although this relative shortness is undoubtedly because of special elongation of the distal segments. The fact is significant that the humerus of *Nesochen* is 16 per cent shorter than in *Branta* and *Anser* in relation to the femur which, in each of these genera, is in turn of about equal proportions to the rest of the body. This figure can be used as a definite value for the degree of reduction in the wing of this insular form.

*Ulna*.—This element is similar in most respects in the various geese. The olecranon is more rounded and less deflected from the line of the shaft in *Nesochen* than in the others and the secondary papillae are weaker. Further, the two intermuscular lines of the radial surface of the proximal part of the shaft are more widely separated. In *Chloëphaga* the external cotyla projects farther distally and has a different distal contour than in the others. At the distal end of the element the only differences lie in the carpal tuberosity. The tuberosity is similar in *Branta*, *Chloëphaga*, *Nesochen*, and *Chen* but averages larger and more extensive proximally in *Anser*.

Length of ulna varies in relation to the humerus as shown in figure 12. *Chen* is decidedly longer proportionately. The others do not differ greatly one from another, with the exception of *Branta c. canadensis* which is remarkably short. In *Nesochen* this segment of the wing is reduced neither more nor less than is the humerus.

*Radius*.—No significant differences were found in this element. Its length of course always corresponds to that of the ulna.

*Carpometacarpus*.—The process which the first metacarpal forms varies in shape; the anterior margin of it may be either straight or concave, irrespective of genus. In *Chloëphaga* the process is more attenuated and longer and the distal margin slightly more concave than in other geese. The tip of the process upon which the extensor tendons attach is subject to much variation. There is usually added to the tip of the process a cap of bone quite evidently formed apart from the remainder of the process and probably laid down in the tendon. Sometimes the cap is smooth but often it is roughened, perhaps through disease as suggested by Shufeldt (1892, p. 408), although I doubt that a structure occurring so frequently could be pathogenic when other parts of the skeleton are not similarly affected. Extreme variation of the cap detracts from the value of the measurements of length of the process. Width across the bone to the tip of the process varies from 22 to 25 per cent of carpo-metacarpal length in all except *Chloëphaga*, in which three specimens are 26, 27, and 30 per cent.

*Branta esmeralda* was described by Burt (1929, p. 222) on the basis of a nearly complete fossil carpometacarpus from the Pliocene. Principal among the characters was the long process formed by metacarpal one which had a prominent tubercle or cap on the end such as described above. Despite this tubercle the process is long and resembles most the genus *Chloëphaga*. I have had the type available for direct comparison. With the tubercle included, width across the fossil bone is 30 per cent of the total length of the bone. The shaft of metacarpal two of *esmeralda* is thicker than in *B. c. leucopareia* (*hutchinsii*) as stated by Burt, but *Chloëphaga* is similar to *esmeralda* in this respect. The greater angle at which the shaft of metacarpal three projects from the distal symphysis in *esmeralda* is a slight difference that does not indicate relationships with any particular species.

The short broad facet for digit three in the fossil is certainly different from other members of *Branta* and from *Anser*, but at least two specimens of *Chen hyperborea* are very similar. In general it may be said that *Chen* has a shorter rounder facet than have the other genera. Characters of the type of *esmeralda*, as here reviewed, leave one somewhat dissatisfied with the generic assignment to *Branta*, yet I hardly feel there is sufficient ground for placing the fossil either in *Chloëphaga* or *Chen*, even though either genus would include it fully as appropriately as does *Branta*. The coracoid referred to *esmeralda*, although not certainly associated with the type, probably came from the same individual. It has none of the very distinct characteristics of the coracoid of *Chloëphaga*. The intermuscular line is like that of *Branta* and there are pneumatic foramina beneath the brachial tuberosity. It has a prominent, inflated anterior end with strong medial overhang and foramina which distinguish it from *Chen*, *Phalacte*, and *Anser*. With the coracoid definitely identifiable as *Branta*, it is best to refer both bones to that genus, because the scanty evidence of relationships of the metacarpus to *Chloëphaga* and *Chen* is based upon characters which seem of lesser stability and which might appear independently in different genera.

Other than the differences in the facet for digit three no differential characters of the distal end of the carpometacarpus were found. *Nesochen* is not distinguishable from the others, but it shows no tendency to have a short facet as in *Chen*.

*Branta howardae* was described by L. Miller (1930, p. 208) from the Pliocene on the basis of a distal end of a carpometacarpus. I am not able to substantiate the generic assignment but likewise have no basis to refute it. The characters of the fossil species have been verified by my reëxamination of the type. One character is the long facet for the third digit set at an angle different from that in other geese and separated by a deep cleft from the facet for digit two. An additional character, an excavation below the condyle on the dorso-ulnar surface also exists. This condition is somewhat different from that in examples of *Branta*, *Anser*, or *Chen*. This excavation is not especially prominent in *Anser* as was suggested by the describer.

Length of carpometacarpus is uniform relative to the humerus except for

*Branta nigricans* in which it is somewhat shorter than in the others. It would appear that, unlike the ulna, the carpometacarpus corresponds to humeral length in *Chen*. In the hind limb it will be recalled that tibia and tarsometatarsus were closely correlated and became lengthened or shortened independently of the femur.

*Phalanges*.—Measurements of the metacarpal digits were taken in the same manner as in the foot, but few significant variations were disclosed. The second phalanx of digit two was similar in its relation to the first in all but *Nesochen* (one specimen) in which it was especially long. Constant differences in shapes of phalanges were not found. Length of the second digit bears a close relation to humeral length. No heterogonic condition was detected as in the foot. In the evolution of this group of birds, wing segments usually have been altered to an equivalent degree with respect to length, as if they constituted a single unit.

*Skull and jaws*.—Although the prime object in comparing the skeletons of geese has been to determine characters and modifications of the limbs and girdles, some examination of the head has been made in order to take account of certain characters that may be important in establishing the relationships of the genera. These will be presented in form of a summary. (See also pl. 6.)

1. Jaws shorter in relation to remainder of skull in *Anser* than in *Chen*; slightly shorter in *Branta*, *Nesochen*, and *Philacte* than in *Anser*; in *Chloëphaga* much shorter than in all others.

2. Bill narrowest in *Chen*; wider in *Chloëphaga*, *Anser*, and *Nesochen*; still wider in *Branta*; widest in *Philacte*. Symphysis of lower jaw broader and more spoon-shaped in broad-billed types.

3. Sides of bill converge most in *Chen*, less so in *Anser* and *Philacte* and least in *Nesochen* and *Branta*. *Chloëphaga* differs from all others in basal lateral compression with slight subterminal expansion.

4. Depth of bill, in middle segment, great in *Chloëphaga* contrasted to others, especially *Branta*.

5. Basal depth of bill relatively less in *Chloëphaga*, *Branta*, and *Nesochen* than in others.

6. Internarial bridge straight (side view) in all except *Chloëphaga*, *B. nigricans*, and *Nesochen*, in which it is convex dorsally; in *B. canadensis*, occasionally slightly concave.

7. Posteroventral process of maxillary narrow and surface vertical in *Chloëphaga*; less so in *Nesochen*; still less in *Branta* and *Philacte*; nearly horizontal and broad in *Anser* and *Chen*.

8. Intermaxillary cleft nearly or entirely closed and usually bordered by "teeth" in *Chen*; cleft broader and without teeth in *Nesochen* and *Anser*; cleft still broader in *Branta* and *Chloëphaga*; broadest in *Philacte*.

9. Dentary concave above and upper surface flattened and inclined laterally in *Chen* and *Anser*; in *Nesochen* and *Philacte* similar but these features not so extreme; in *Branta* upper surface usually not concave and flattened surface less inclined; in *Chloëphaga* surface not concave and not flattened.

10. Surangular-coronoid crest of lower jaw abrupt anteriorly and high throughout in *Chen* (less so in *Chen rossii*), *Anser*, and *Philacte*; less so in *Branta* and *Nesochen*; least in *Chloëphaga*.

11. Internal and postarticular processes of lower jaw and spine on lateral surface of coronoid process more prominent and longer in *Chen*, *Anser*, and *Philacte* than in others, except that in *Nesochen* internal articular process is long.

12. Anterior process of lacrimal extremely long in *Chloëphaga*; much shorter, but projecting well forward, in *Branta* and *Nesochen* in which lacrimals are strikingly similar in shape; process still shorter in *Chen*, *Anser*, and *Philacte*; shape in latter three differs in minor respects.

13. Lacrimal and frontal inflated in *Chloëphaga leucoptera* but apparently not in all other members of genus nor in other geese.

14. Orbital process of lacrimal long in *Chloëphaga*, forming an almost complete subocular bar as in the tree-ducks; this condition not approached in other geese.

15. Orbital process of lacrimal broad in *Chen* and *Anser*; narrow in *Branta* and *Philacte* and especially in *Nesochen*.

16. Impression of nasal gland in frontals small in *Nesochen*, *Anser*, *Chen*, and *Chloëphaga leucoptera*; intermediate in *Branta c. minima*; broad in *Branta nigricans*; equally broad and differently shaped in *Philacte*. Schildmacher (1932, pp. 293-299) has shown that nasal glands and skull depressions for them may be altered by environment, namely, salt or fresh water conditions, even in mature individuals; salt water forms have larger glands.

17. Palatines extremely long in *Chloëphaga*; much shorter in others, especially *Nesochen* and *Philacte*.

18. Opisthotic process longer in *Chen*, *Anser*, and *Philacte* than in *Nesochen*, *Branta*, and *Chloëphaga*.

#### EXTERNAL CHARACTERS

The studies that Alpheraky (1905) and others have made have been of great aid in selecting for consideration characters of plumage, bill, and feet that are particularly pertinent in analyzing relationships of the larger subdivisions of the Anserinae. Alpheraky based the major divisions of his keys upon tail, bill, and foot color, feather margin at base of bill, fluting of feathers of the neck, and length of the hind toe. To these should be added the exposure of the maxillary "teeth."

The bills of *Branta*, *Nesochen*, and *Chloëphaga* are black; in other genera the bills are either reddish, orange, or yellow with various black, white, or dusky spots. The maxillary "teeth" are not exposed laterally in *Chloëphaga*. They may be seen rarely in some individuals of *Branta* and *Nesochen*; in *Philacte* they are always exposed basally and in *Anser* and *Chen* are well exposed throughout. This character is closely associated with the nature of the dorsal surface of the dentary and with the shape of the posteroventral process of the maxillary.

The pointed feather outline at the base of the culmen, characteristic of *Branta*, is not found in *Nesochen* or in the others.

The feet of *Nesochen* and *Branta* are black, whereas they are orange, yellow, or pink in other genera. The plantar pads of the foot are most prominent in *Nesochen*; in the others they are decidedly thinner, although *Chloëphaga* shows some approach to the condition in *Nesochen*. In the island goose the thick pads should be of advantage in the lava fields which they inhabit.

The web of the foot is decidedly reduced in *Nesochen* (see fig. 2). The other geese have full webbing, although in *Chloëphaga leucoptera* there is some slight incision of the web, in so far as may be determined from dried and folded feet. The least extent of the outer web with toes separated is but 53 per cent of middle toe length in *Nesochen* compared with 76 per cent in *B. c. minima* and 78 in *B. nigricans*. The inner web is comparably reduced. The webbing in the Hawaiian Goose is reduced, consequently, about 31 per cent compared with *Branta*. This is the most striking external character of the genus; it was appropriately selected by Salvadori (1895, p. 81) as the chief distinguishing character at the time he erected the genus. The toes of *Nesochen* have elongated distally and appear literally to have left the web behind. Regardless of whether the webs have been actually or only relatively reduced, there is no reason to assume that the web was reduced because of disuse. There would be distinct advantage in the matter of freedom of the toes and freedom from web injuries on the lava in the reduced extent of webs.

The feathers of the neck of *Nesochen* are conspicuously fluted so that stripes of the darker feather bases are exposed. It is claimed that they are provided with an oily aromatic substance. Some fluting is present in *Anser* and *Chen*; it is not wholly lacking in *Branta*, but seems to be absent in *Chloëphaga* and *Philacte*.

The tail of *Nesochen* and *Branta* is solid black with white upper coverts; in *Anser* the rectrices are dark brown with white tips and the upper tail coverts are white; in *Chloëphaga* the pattern is variable; in *Chen* and *Philacte* the tail is principally white.

The body coloration of *Nesochen* resembles *Anser* and *Branta* about equally. There is none of the fine barring and mottling suggestive of *Chloëphaga* and *Philacte*.

The head coloration of the adult Hawaiian Goose is similar in pattern to *Branta canadensis* but differs in that light areas (creamy) extend to the entire ventral part and sides of the neck instead of being limited to a cheek patch. The ventral margin of the light-colored cheek patch slants back from the eye rather than forward beneath it as in *B. canadensis*. The chin and upper throat are not white as in *canadensis*. The same tendency for a black breast band to appear separating throat and breast occurs in *Nesochen* and *Branta*. This latter feature and the white cheeks and black pileum common to the two do not appear in *Anser*. *Nesochen* has no suggestion of white frontal markings. The juvenal *Nesochen* is instructive in that it resembles *B. canadensis* more than does the adult. The white on throat and head is limited to a cheek patch

as in *canadensis*, although the patch is shaped ventrally as in the adult *Nesochen*. The juvenile does not have the breast band, but does possess distinctly black pilium and dorsal neck stripe.

### DISCUSSION OF RELATIONSHIPS OF GENERA

In order to unify my concepts of the many likenesses and differences ascertained in the foregoing studies of skeleton, musculature, and external anatomy, I have found it necessary to devise a method of summing differential characters. As a preliminary step, each character that displayed other than individual and age differences was set down, irrespective of apparent importance, in a brief empirical phrase or formula. Three examples follow :

M. gluteus minimus—origin extends far anterior in *Nesochen* > (less so in) *Branta* > *Chen* >> (much less so in) *Anser* and *Philacte*.

M. extensor femoris—bulk in *Nesochen* > *Branta c. minima*, *Anser*, and *Chen* > *Philacte* > *Branta nigricans*.

Femur—rotular groove narrow, outer surfaces of condyles converging in *Chen* > *Anser*, *Branta*, and *Philacte* > *Nesochen* > *Chloëphaga*.

Sometimes the genera were arranged more or less in series as in these examples, but in others one genus stood in contrast to all the others. This method of summarizing tells little concerning the real nature of the differences and does not present to the reader an easily comprehended view of the differences. But, the formulae have been useful to me in showing how frequently one genus was grouped with another with respect to differential characters.

Formalized statements of this type pertaining to differences in muscles, inclusive of leverage, but exclusive of bulk, totaled 33; for muscle bulk, 11; for the skeleton, head included, 61; for external features, 10. A grand total of 115 differential characters resulted.

The inequality in values of these 115 characters cannot be too greatly stressed. Some characters involve parts that evidently are capable of rapid evolutionary change, such, for example, as muscle bulk; there is even some doubt as to the degree to which this is hereditary. Many characters may be classed as of current adaptive value (cenotelic) but these may be, nevertheless, distinctly useful and reliable in showing the relationships of lesser taxonomic groups. Adaptations may be of current survival value and yet have great antiquity. Still other characters seem to have no special adaptive value at present. The stress that should be placed upon them is largely a matter of personal opinion. Some such characters are of great antiquity but others may recently have been swept into the genetic complex of the species linked to an adaptive character that perhaps was purely functional in nature. Characters, currently nonadaptive, and equally manifested in several distinct species must of course be of decided antiquity (paleotelic). If one classifies characters as to value there almost inevitably is injected to a noticeable degree the investigator's personal theory and bias as a means to arranging the facts. This procedure often departs too completely from the inductive method.

When a large number of characters is available, sheer quantity should point

out the resemblances and differences and, to a degree, the genetic relationships of the genera. I propose, therefore, to treat all characters in equal fashion to begin with and then modify, where necessary, the conclusions drawn on this basis through consideration of the values of the characters. An artificial resemblance or relationship score was drawn from the 115 empirical statements in the following manner. Whenever two forms possessed a character, or phase or degree of character, in common to the exclusion of other species, 2 points were accredited their relationship score; 1 point was given when the two possessed the same character but in common with some other species; when several forms were arranged in series, each somewhat different, 1 point was given to the relationship of the two standing in juxtaposition in the series. The resulting scores appear in table 8.

TABLE 8  
RELATIONSHIP SCORES

|                                | <i>Nesochen</i> | <i>B. c. minima</i> | <i>B. nigricans</i> | <i>Branta</i><br>(2 species) | <i>Philacte</i> | <i>Anser</i> | <i>Chen</i> |
|--------------------------------|-----------------|---------------------|---------------------|------------------------------|-----------------|--------------|-------------|
| <i>Nesochen</i> .....          | ..              | 54                  | 45                  | 48                           | 30              | 28           | 28          |
| <i>B. c. minima</i> .....      | 54              | ..                  | 103                 | ..                           | 56              | 54           | 48          |
| <i>B. nigricans</i> .....      | 45              | 103                 | ..                  | ..                           | 60              | 54           | 51          |
| <i>Branta</i> (2 species)..... | 48              | ..                  | ..                  | ..                           | 54              | 49           | 50          |
| <i>Philacte</i> .....          | 30              | 56                  | 60                  | 54                           | ..              | 75           | 70          |
| <i>Anser</i> .....             | 28              | 54                  | 54                  | 49                           | 75              | ..           | 85          |
| <i>Chen</i> .....              | 28              | 48                  | 51                  | 50                           | 70              | 85           | ..          |

Separate relationship scores based only on skeletal and external characters (71) must be used to show the relationships of *Chloëphaga*, since the musculature of this genus was not studied. These scores relating *Chloëphaga* to the others are: *Nesochen*, 20; *Branta*, 24; *Philacte*, 26; *Anser*, 18; and *Chen*, 19. For purposes of comparison the scores for *Anser* based on the same 71 characters are: *Nesochen*, 25; *Branta*, 35; *Philacte*, 46; and *Chen*, 56.

The index of relationships for the two species of *Branta* is exceedingly instructive. It is apparent from the analysis of the hind limb that *nigricans* and *minima* are quite differently adapted, yet no one will seriously doubt the natural relationship of the two. Their relationship index is 103, much higher than that for any other two forms in the table. The points wherein they differed were almost all characters having to do with muscle bulk, leverage, and proportions of limb segments. Most other characters of musculature and skeleton were classed as the same in these two. Naturally this evidence points the way to the kinds of characters that are fundamental and conservative in evolution.

This information was used extensively in evaluating characters. It served to bring into prominence such features as the shape of the distal end of the tarsometatarsus in *Philacte* and *Chloëphaga*, the separation of the heads of the *M. flexor perforatus medius primus pedis* in *Nesochen* and the overlap of the origins of the *M. gluteus primus* and *M. biceps femoris* in *Nesochen* and



*Branta*. Each relationship score was examined in all its component parts and a more or less revised opinion of affinities derived.

*Nesochen* is most closely related to *Branta*, but it is as distinct from *Branta* as is *Chen*. The resemblance of *Nesochen* to *Branta c. minima* is greater than to *nigricans*, but this is almost entirely on the basis of less fundamental characters that may have evolved in parallel fashion. There is no close relationship indicated between *Nesochen* and other genera, although I feel that *Anser* is less remote from the Hawaiian Goose than are *Chen*, *Philacte*, and *Chloëphaga*.

*Branta* is similarly related to *Philacte*, *Anser*, and *Chen*, although perhaps slightly more to *Philacte*.

*Philacte* is close to *Anser* and *Chen*, much more so than to *Branta*.

*Anser* and *Chen* are the most closely related of all the genera and their relationships to other genera are highly similar throughout.

*Chloëphaga* stands apart from the other geese fully as much as does *Nesochen*. The relation of *Nesochen* and *Chloëphaga* is not high despite some parallel adaptations in the foot. The closest relationship of *Chloëphaga* among the genera studied is with *Branta* and *Philacte*, especially the latter; the relationship figure is too low in this instance in the light of the importance of some of the characters held in common. Nevertheless, *Chloëphaga* probably will prove to be more closely related to some other anserine than to any of the North American forms.

Although these conclusions point to community of blood relationships and of origin, these facts cannot be stated with finality. We are studying here six genera of geese, terminal twigs of an evolutionary tree spread out in three dimensions. It is extremely difficult, especially without the aid of ontogenetic data or pertinent paleontological evidence, to know precisely how the twigs arose at the base of the bush or tree. One can surmise that *Branta* represents one main central branch with the *Philacte-Chen-Anser* stock representing another branch, and that *Nesochen* early diverged from the holarctic genus *Branta*. *Chloëphaga* probably had early origin as still another main division of the subfamily Anserinae.

## SYNOPSIS OF ADAPTIVE EVOLUTION IN GEESE

The earliest known fossil geese were not strikingly different from modern geese. They afford no good evidence to show whether modern geese as a group have become more or less terrestrial than their immediate ancestors. In contrast to the ducks, geese are viewed as the chief terrestrial branch of the Order Anseriformes. The primitive and generalized anserines are swimmers so that a land-adapted form like *Nesochen* is assumed to be a specialized type, not ancestral. The problem remains: Were the immediate ancestors of the subfamily Anserinae like *Branta nigricans* or like *Branta canadensis* in the matter of specialization? Since the majority of geese, living and fossil, are more like the latter, the assumption is made for purposes of discussion that the condition in *Branta canadensis* is similar to that of the ancestors of the living

genera and species; I think this point cannot be proved from known evidence.

The geese available permit the tracing of lines of adaptation in closely related forms so that details in the process of adaptation may be witnessed. This situation would seem to have some advantages over a comparison merely of widely separated forms, the nature of whose adaptations may be confused by nonadaptive characteristics peculiar to the different families concerned. At least four adaptive trends must be recognized in the limbs of geese: adaptation for walking and running; specialization for climbing (not arboreal); increased specialization for swimming, or, perhaps, merely retention of swimming power with loss of ability on land; increase or decrease in power of flight.

*Walking and running.*—Among the forms studied, *Nesochen* represents the extreme of this type of specialization. *Branta c. minima*, *Chen hyperborea*, *Chen rossii*, and *Chloëphaga leucoptera* show certain modifications in the same direction, each possessing some characters, but usually not exactly the same characters, that indicate this adaptive trend.

Structural features correlated with walking and running ability are: increase of total leg bulk relative to the body; increase of range of action in the M. gluteus medius, M. gluteus minimus, and iliac head of the M. caudofemoralis; large M. satorius which is of use both in propulsive and recovery strokes; large M. gluteus primus and M. extensor femoris together with a broad rotular groove of the femur, the muscles serving importantly in running and jumping; lever arrangements associated with the M. biceps, M. gastrocnemius and M. tibialis anticus designed for speed rather than power; relative enlargement of the tibial head of the M. gastrocnemius, the most efficient head in the act of running; increased strength of certain tendons of the toes; increase in bulk of the M. peroneus longus, useful in preventing toeing-in; straight tarsal and tibial shafts; elongation of the tibiotarsus and tarso-metatarsus; relative shortening and compacting of the foot, except where climbing and running adaptations both are present; and large plantar pads.

*Climbing.*—This adaptation in geese pertains merely to ability to progress over steep or irregular ground. It is an adaptation peculiar to *Nesochen* among the species under consideration. Characters correlated with habit and action in the Hawaiian goose are: flexibility of toe action made possible by long bellies of toe flexors and separation of the heads of certain of these muscles; great strength of tendons to toes; flexibility and independence of toe action through enlargement of the short toe flexors; elongation of the toes; partial freedom of toes from the web; large plantar pads as protection on the lava rocks; and large nails.

*Swimming.*—Modification for swimming is most pronounced in *Branta nigricans*. In many respects *Philacte canagica* and *Anser albifrons* approach *B. nigricans* and may even surpass it. Most features that can be correlated with swimming in these geese are not of an extreme nature. Swimming power is retained in them without loss through the alterations necessary for running power. It comes into prominence in them possibly by reason of reduction of

running ability. None of these geese is comparable to the swimming and diving anseriformes such as the scoters, *Oidemia* and *Melanitta*, or the fossil diving goose, *Chendytes*.

Features associated with swimming power are: great relative bulk of the *M. biceps femoris*, *M. semitendinosus*, and *M. semimembranosus*, important in bracing tibiotarsus during the power stroke; large size of the external head of the *M. gastrocnemius*; leverage of actions of the *M. biceps*, *M. gastrocnemius*, and *M. tibialis anticus* designed for power movements in the resistant medium; posterior position of the origin of the *M. semitendinosus* which provides more powerful leverage; elongation of toes; and complete webbing of the three major digits.

The legs are relatively short, but shortening has taken place in the tibial and tarsal segments. This makes the femur appear relatively long which is a reversal of the tendency to shorten the femur seen in extreme aquatic adaptations, especially diving forms (see Dabelow, 1928, p. 301, and Stolpe, 1932, p. 226-227). I interpret the relatively long femur in these swimming geese not as a positive alteration useful in swimming but merely as the absence of elongation of distal segments for purposes of running; the femur is long only when compared with the running type. Specialization for swimming among the living geese has not progressed far enough, especially with respect to the diving phase, to bring about the shortening of the femur unquestionably associated with extreme aquatic adaptation. In like manner there is no pronounced narrowing of the pelvis and enlargement of the cnemial crest that Dabelow and others have pointed out in aquatic specialization.

*Flight*.—Especially powerful flight, that is, strength of wing beat, is found in *Chloëphaga leucoptera*. In this species the wing is not as long as in some of the North American land geese such as *Chen hyperborea* which may be the best adapted for sustained flight. *Branta nigricans* and *Phalacrocorax auritus* are weaker fliers. *Nesochen* has the weakest flight apparatus, definitely suggesting degeneracy of the wings. The relationship of *Nesochen* with *Branta* favors a theory of degeneracy rather than preservation of a primitive state of weak flight. Features associated with flight power are: width of the sternum; lateral shifting of the intermuscular line on the ventral surface of the coracoid (increase of the *M. pectoralis secundus* at the expense of the *M. pectoralis tertius*); deep impression of the *M. triceps* on the head of the humerus; strong deltoid crest of the humerus; elongation of the wing segments; and relatively long ulnar segment. It is possible that some differences in muscle bulk may exist in the fore limb.

*Resumé of types of adaptations in the genera*.—*Nesochen* is well adapted for running, jumping, and climbing on rough steep terrain. The hind limb as a whole has increased 25 per cent in comparison with those of related North American forms. There has been a reduction in swimming and flying power, in the latter to the extent of about 16 per cent compared with that of *Branta*. Many structural characters in the muscular and skeletal apparatus correlate positively with known habits of this peculiar insular goose.

*Chloëphaga leucoptera* combines cursorial adaptation with retention of swimming ability. Knowledge of the musculature is much to be desired in this connection. The wing apparatus is especially powerful.

*Chen hyperborea* (probably also *Chen rossii*) is almost as much specialized for running as is *Branta c. minima*. The wing is long and powerful. Swimming ability is retained.

*Anser albifrons* is not well adapted for running but is a strong swimmer. It possesses moderate flight power.

*Philacte canagica* is not well adapted for running but is a strong swimmer. Flight is relatively weak.

The range of adaptive modification within the genus *Branta* is great with respect to certain plastic features such as muscle bulk, limb length, and leverage. The differences may be as great as those between certain of the genera. But, in the conservative aspects of skeletal configuration, divisions of muscles and positions of muscle attachments, differentiation within the genus has been slight. *Branta nigricans* is poorly adapted for running but is a strong swimmer. Flight is relatively weak. The races of the Canada goose, *Branta c. canadensis*, *B. c. leucopareia*, and *B. c. minima*, show progressively greater modification for running and lesser modification for swimming. All are powerful fliers.

A point to be emphasized is that a single modification, important in a given type of adaptation, is not equally manifested in all the species that display a comparable degree of that adaptation. For example, *Anser albifrons*, *Philacte canagica*, and *Branta nigricans* seem to me about equally suited for swimming activity. But one of these may be most modified with respect to some feature of leverage, another with respect to muscle bulk, and the other with respect to length of limb segments. Similarly, *Chen hyperborea* and *Branta c. minima* are alike with respect to running power but not identical in all features contributing to the adaptation. Adaptive evolution in accomplishing certain ends does not in each species follow precisely the same pathway.

## SUMMARY

The muscular and skeletal anatomy of the Hawaiian goose (*Nesochen sandvicensis*) and of North American representatives of the genera *Branta*, *Chen*, *Anser*, and *Philacte* has been studied. Skeletal material of the South American genus *Chloëphaga* was used. Particular attention has been directed to the hind limb, and a full description and comparison of its musculature is presented.

A physiological-anatomical analysis of limb mechanics has been attempted with especial reference to the musculature. Through this analysis it has been possible to correlate certain pronounced differences in bulks of muscles with habits and the natural history of the species. Other differences in musculature and in skeleton likewise are correlated with actions and movements observed in these birds. Three sets of differences in lever action in the limbs have been calculated.

The Hawaiian goose is peculiarly adapted for life on the dry lava uplands of the island of Hawaii. Its structure is modified for running and climbing over rough ground. Swimming power and especially flight power are materially reduced. Other species of geese examined have become specialized to lesser degree for walking and running; *Branta nigricans*, *Philacte canagica*, and *Anser albifrons* have retained, or perhaps augmented, their proficiency in swimming.

Characters differentiating the species of geese total 115. This total includes features believed to be adaptive. A method for determining relationships was devised which yielded a relationship index for each form with respect to the others. From this and other evidence it is concluded that *Nesochen* is related to *Branta* but that it constitutes a well-marked, monotypic genus as distinct from *Branta* as is *Chen*. *Anser* and *Chen*, and to a less degree *Philacte*, are closely related. *Anser albifrons* and *Chen hyperborea* are not as closely related, however, as *Branta nigricans* and *Branta c. minima*. *Chloëphaga* is not closely related to North American geese or to *Nesochen*. The generic affinities of several fossil geese are discussed.

*Nesochen* most probably arose from *Branta* stock. Anatomical characters of a nearly full-grown juvenal bird do not furnish clues concerning ancestry. The color pattern of the juvenile suggests *Branta*.

In adaptive evolution some structures are more plastic than others. But, in the degeneration of the wing of *Nesochen* the various parts seem to have been affected almost equally. The reduction of the webs of the feet in *Nesochen* may have positive value in its upland habitat and cannot be attributed merely to disuse. The principle of heterogonic growth is applicable to modifications in toe length. Species in related genera do not attain similar adaptations in precisely the same manner.

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*Transmitted December 1, 1934.*

## EXPLANATION OF PLATES



## PLATE 1

*a, b, c, and d.* Femora, anterior view, showing differences in width of rotular groove. All approximately  $\times \frac{1}{6}$ .

*e, f, g, h, i, and j.* Femora, posterior view, showing differences in popliteal area and in head and neck. All  $\times \frac{2}{3}$ .

*a, e.* *Chen hyperborea hyperborea*, no. 22446 M.V.Z.

*b, f.* *Branta canadensis leucopareia*, no. 22453 M.V.Z.

*c, h.* *Nesochen sandvicensis*, no. 60896 M.V.Z.

*d, j.* *Chloephaga leucoptera*, no. 227054 U.S.N.M.

*g.* *Nesochen sandvicensis*, no. 60923 M.V.Z.

*i.* *Phalacte canagica*, no. 1499 coll. James Moffitt.



## PLATE 2

*a, b, c, d, and e* Tibiotarsi, anterior view, showing differences in fibular crest and in medial displacement of condyles. All  $\times$  -

*f* and *g* Pelvis, lateral view, showing differences in contour and in size of ilio ischiatic fenestra. Approximately  $\times 7_{11}$

*a* *Anser albifrons gambelli*, no. 46018 M V Z

*b* *Anser albifrons albifrons*, no. 1979 A H M

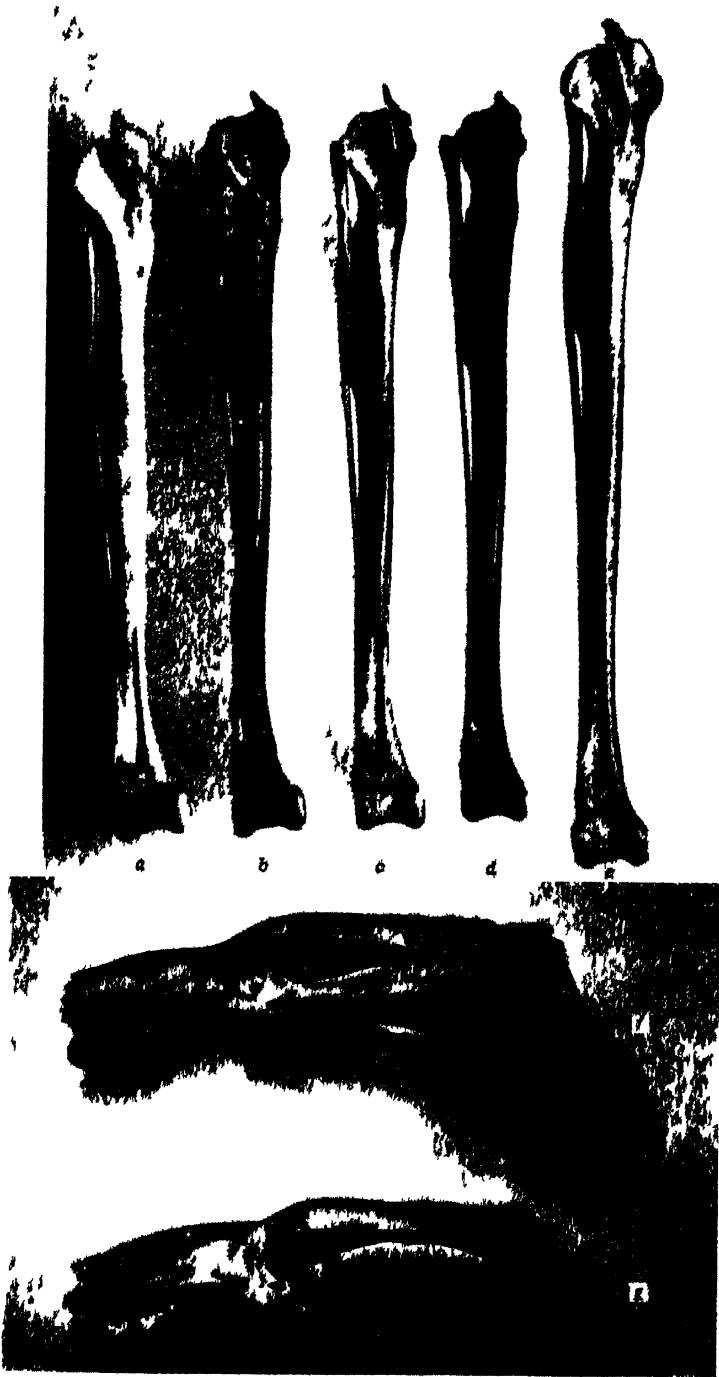
*c* *Nesochen sandvicensis*, no. 60896 M V Z

*d* *Nesochen sandvicensis*, no. 60923 M V Z

*e* *Chloephaga leucoptera*, no. 227054 U S N M

*f* *Chen hyperborea hyperborea*, no. 56270 M V Z

*g* *Nesochen sandvicensis*, no. 60896 M V Z



*a b c d* and *f* Trisometritis posterior view, showing differences in shape of trichilei for digit two and in plantar surface proximal to trichilei. All approximately  $\times 5$ .

*g h i j l* and *l* Trisometritis interior view, showing differences in tendinal groove and in shape of proximal end. All

*a g* *Biantia canadensis leoparata* no. 2245 M V Z

*b h* *Inser albifrons albifrons* no. 1979 A H M

*c i* *Nesochen sandvicensis* no. 60596 M V Z

*d j* *Cuen hyperborea hyperborea* no. 54632 M V Z

*e l* *Chloephaga leuceptera* no. 227054 U S N M

*f l* *Phlaeete canugica* no. 55450 M V Z



PLATE 4

*a, b, c, and d* Humeri, anconal view, showing differences in depression for attachment of *M. triceps*. All  $\times 4$

*e, f* and *g* Sterna, dorsal view, showing differences in pneumatic foramina and in manubrial spines. Approximately  $\times 1\frac{1}{2}$

*a* *Chloeophaga leucoptera*, no. 19731 U S N M

*b* *Branla canadensis minima*, no. 22458 M V Z

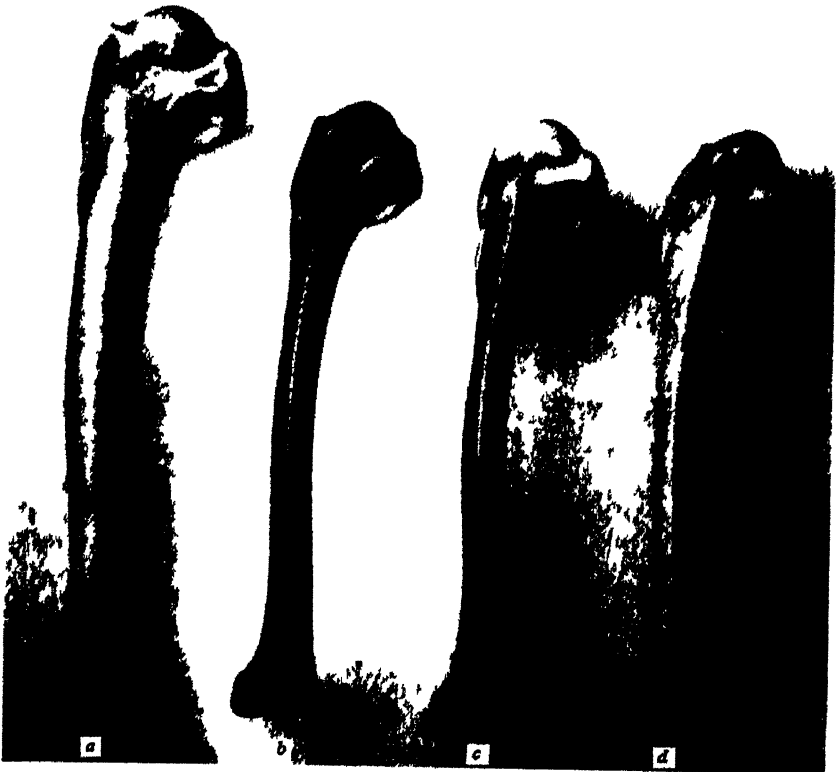
*c* *Nesochen sandvicensis*, no. 60896 M V Z

*d* *Chen rossii*, no. 46026 M V Z

*e* *Nesochen sandvicensis*, no. 60896 M V Z

*f* *Anser albifrons albifrons*, no. 27582 M V Z

*g* *Chloeophaga leucoptera*, no. 19731 U S N M





## PLATE 5

*a, b, c, d,* and *e* Coracoids ventral view. Note position of intermuscular line on shaft which indicates development of flight power (see p. 51). All  $\times 3$ .

*e, f, g, h,* and *i* Coracoids dorsal view, showing differences in tubercles and pneumatic foramina. All  $\times 3$ .

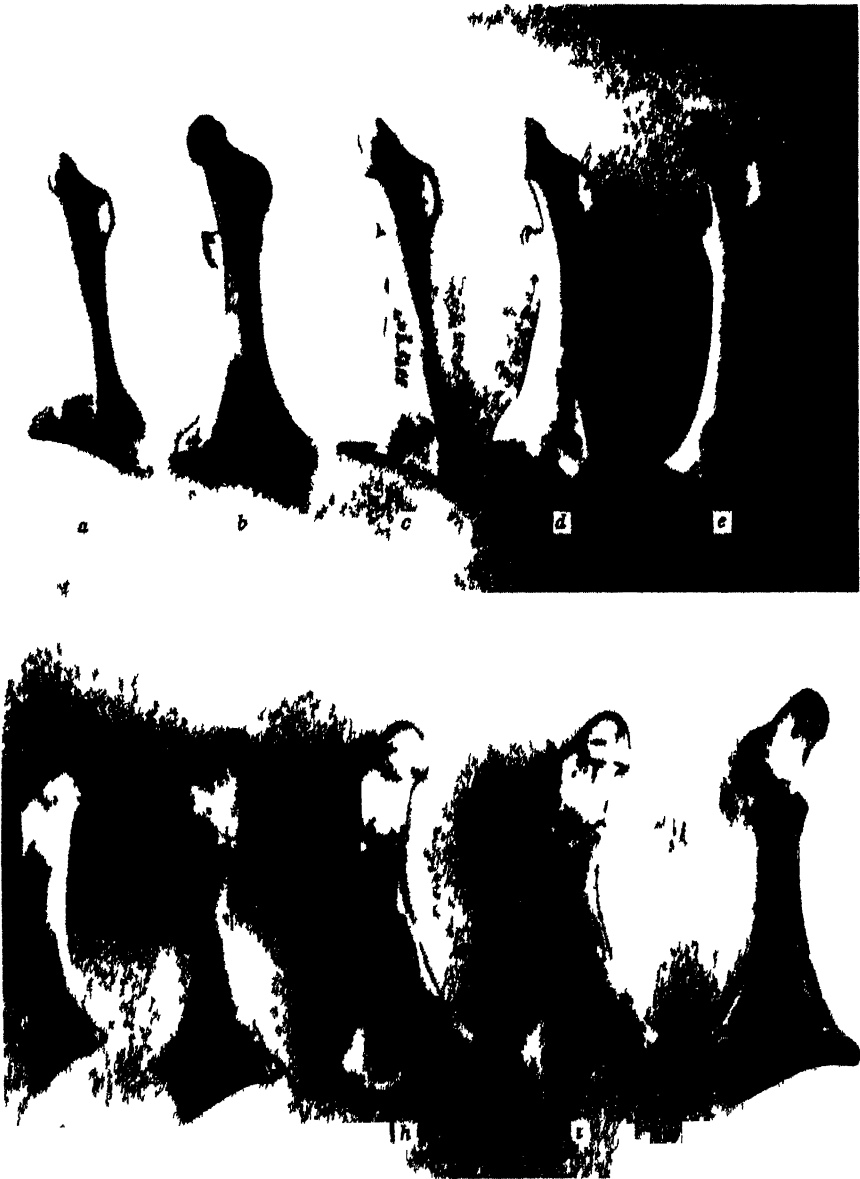
*a, e* *Desothen sandicensis*, no. 60896 M V Z

*b, f* *Branta canadensis leucoparva* no. 22453 M V Z

*c, g* *Anser albifrons albifrons*, no. 53759 M V Z

*d, h* *Chen hyperborea hyperborea* no. 28993 M V Z

*e, i* *Chloephaga leucoptera* no. 19731 U S N M



# PLATE 6

a b c d, e, and f Skulls, dorsal view, showing shapes of bills and differences in the depressions for the nasal glands All  $\times \frac{1}{2}$   
 g h i j l and l' Skulls, lateral view showing differences in shapes of lacrimals and maxillaries All  $\times \frac{1}{2}$

a i *Anser albifrons gambelli* no 46018 M V Z

b h *Chen hyperborea hyperborea*, no 45555 M V Z

c g *Chloephaga leucoptera* no 19731 U S N M

d l *Nyroca sandvicensis* no 59136 M V Z

e *Branta nigricans* no 52811 M V Z

f j *Phalacrocorax auritus*, no 54483 M V Z

k *Branta canadensis minima* no 22459 M V Z





MORPHOLOGY OF THE POCKET GOPHER  
MAMMALIAN GENUS THOMOMYS

BY  
JOHN ERIC HILL

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# MORPHOLOGY OF THE POCKET GOPHER MAMMALIAN GENUS THOMOMYS

BY

JOHN ERIC HILL

(Contribution from the University of California Museum of Vertebrate Zoology)

## INTRODUCTION

THE AIMS OF THE PRESENT INVESTIGATION have been five in number: first, to describe the gross anatomy of the pocket gopher, exclusive of what has been previously described; second, to inquire into the phylogenetic relationships of this rodent as indicated by its structure; third, to collect the results of recent work in mammalian anatomy and apply them to the interpretation of the structure of the pocket gopher; fourth, to obtain evidence that might confirm or contradict the conclusions of other authors regarding the homologies of mammalian structures; and last, to consider the anatomical features that have evident and special adaptive significance.

The gross anatomy of many of even the commoner rodents is still incompletely known, although in recent years there has been a revival of interest in morphology. And certain parts of the anatomy of the pocket gopher, the teeth, the skull, and the myology and osteology of the forelimb have been described. Other described details of the anatomy of the pocket gopher are referred to in the text, but taken together all that has been published does not approach a complete description of the structure of this specialized animal.

The author is indebted to those in charge of the Museum of Vertebrate Zoölogy, University of California, for the use of skeletal materials and preserved specimens forming parts of its collections; to Mr. Charles D. Bunker, Assistant Curator of the Museum of Birds and Mammals, University of Kansas, for skeletons of *Cratogeomys*; and to Mr. Claude W. Hibbard, of the same institution, for preserved specimens of *Geomys*. The author is also under obligation to Professors J. Frank Daniel, Joseph Grinnell, E. Raymond Hall, and Ian M. Thompson, of the University of California, for their criticism and guidance throughout the course of the present study. Certain notes on limb bones of rodents made by Mr. Reuben A. Stirton, of the Department of Paleontology, University of California, suggestive of productive lines of investigation, were freely placed at the writer's disposal. Mrs. Frieda Abernathy and Miss Margaret Wythe gave valuable assistance by suggestions and criticism during the preparation of the illustrations.

The materials which were used in this study comprised the following species:

*Thomomys bottae* (Eyndoux and Gervais), from Berkeley, Alameda County, California, twenty preserved specimens and eight skeletons.

*Thomomys bulbivorus* (Richardson), from Hillsboro, Washington County, Oregon, nine preserved specimens and four skeletons.

*Geomys bursarius* (Shaw), from Lawrence, Douglas County, Kansas, eight preserved specimens and four skeletons.

*Cratogeomys castanops* (Baird), from Carlsbad, Eddy County, New Mexico, four skeletons.

*Citellus richardsoni* (Sabine), from near Brandon, Manitoba, Canada, one preserved specimen and two skeletons; Chester, Liberty County, Montana, one preserved specimen.

*Sciurus griseus* (Ord), from near Newberg, Yamhill County, Oregon, one preserved specimen; Los Angeles County, California, one skeleton.

*Aplodontia rufa* (Rafinesque), from near Oregon City, Clackamas County, Oregon, two preserved specimens; near Marshfield, Coos County, Oregon, three skulls; Marin County, California, two skeletons.

*Dipodomys spectabilis* Merriam, from near Tucson, Pima County, Arizona, three preserved specimens.

*Neotoma fuscipes* Baird, from Berkeley, Alameda County, California, one preserved specimen and two skeletons.

*Rattus norvegicus* (Erxleben), from Berkeley, California, one embalmed specimen.

Additional material, as mentioned in the text, was examined in connection with the skeletal system.

The terminology used is that of the international system (B. N. A.) or the English equivalents, employed in modern human anatomy, except where certain names are misleading when applied to mammals other than man. In this connection it seems desirable to replace in description, except where no change of meaning is involved (as, for example, in connection with the structures of the head), the terms "anterior," "posterior," "superior," "inferior," by those of more general application, namely, "ventral," "dorsal," "cranial" or "cephalic," and "caudal." It also seems advisable to restrict the adverbial form of these words, namely, that ending in "-ally" (for example, ventrally) to references to *position*, and to use the form ending in "-ad" (for example, ventrad) when *course* is intended (cf. Bensley, 1926, p. 43).

## EXTERNAL CHARACTERS

Pocket gophers are rodents of moderate size, with a stout body, short legs, and small eyes and ears. General shape fusiform; head large; cervical constriction practically absent. Skin loose, capable of stretching; over most of the body it is thin and easily torn, which may be an advantage in escaping enemies, but around the head it is thicker and on the throat the dermis is greatly thickened and strengthened, especially in males. The additional thickness may be for the protection of these regions in fighting; pocket gophers are very pugnacious, and the external jugular vein is large and entirely superficial.

The pelage consists of fine silky hairs of moderate length, longer in winter. In *Thomomys* there are scattered guard hairs of noticeable length, especially in the rump region, which resemble the spiny hairs of some pocket mice (subgenus *Chaetodipus*) but are much less developed.

Immature animals have longer, softer hair than do adults; a postjuvenile molt begins about the time the young animals begin to shift for themselves.

The tactile vibrissae are similar to those of most rodents (Pocock, 1914), but in pocket gophers interramal and carpal vibrissae are absent. Both of

these are well developed in squirrels and in *Aplodontia*. Long guard hairs on the rump and elsewhere probably serve as sensory organs, particularly in retrograding inside the burrow. In *Thomomys* there is a thick fringe of bristles on radial side of first two digits, with less developed tufts on radial side of other digits, and on ulnar side of pollex and second digit. These fringes aid in preventing dirt from slipping between the digits when the pocket gopher is pushing it from one place to another. Similar fringes occur in the hind foot on both sides of the toes, but there are fewer and weaker hairs. Eyelashes little, if any, longer than hair of adjacent facial region.

Mammae vary in number from two to seven pairs in the different species. *Thomomys bulbiworus*, and *Thomomys bottae*, have usually only four pairs of mammae, two pectoral, two inguinal, but the latter form may have as many as six pairs.

Two halves of upper lip meet below the rhinarium, forming a short median philtrum. In *Thomomys* this is short and naked; longer and slightly haired in *Geomys*. Palatal lobes of the upper lip meet and fuse behind the incisors much as in the unrelated fossorial genera *Ellobius*, *Heliothobius*, and *Heterocephalus* (Vinogradov, 1926). This is doubtless an adaptation to prevent dirt from entering the mouth when the incisors are used in digging operations (cf. Merriam, 1895). Lobes of lower lip closely approximated behind the lower incisors, but do not fuse. Lower lip free for some distance; may be retracted by a slip of *M. platysma* in gnawing, exposing bases of incisors.

Rhinarium naked, triangular, with apex directed ventrally. External nares open anterolaterad; their margins scroll-like, beginning at the dorsolateral angles, forming incomplete figure 6's. Between the nares, a deep internarial groove, continuous with philtrum of the upper lip. In *Geomys* a dorsal limiting groove above the rhinarium; above this, a thickened pad; anterior part of pad nearly naked. The rhinarium in pocket gophers is more like that in muroid rodents such as *Rattus* and *Microtus* than like that in any of the squirrels (Pocock, 1922), whereas *Aplodontia* agrees closely with the sciuroid forms in this character.

Eyes small, weak-looking, as is usual in fossorial mammals. Conclusions drawn from the behavior of live pocket gophers agree with the anatomical indications that these animals are very near-sighted. Lens nearly spherical, very large in comparison to the eye bulb. Pupil round. Iris dark brown, almost black. Well-developed lacrimal glands, one lobe outside orbit near the ear, supply a thick milky fluid which cleanses the cornea. Fossorial mammals frequently get dirt in the eyes; protection of this nature is needful. Nictitating membrane vestigial, a small, pigmented, knoblike structure in the anterior angle of the eye slit.

Auricula small and rounded. It is possible to make out some of the typical mammalian structures, although these are of a vestigial nature. Anterior part of helix folded, much as in *Dipodomys* (Howell, 1932). Antihelix forms a ridge margining conchal cavity. In *Thomomys* a small antitragus is present on posterior side of intertragical notch, opposite this a fairly distinct tragus.

Neither of these is distinguishable in *Geomys bursarius*. Lower border of auricula, caudal to antitragus, slightly thickened and rounded, somewhat like the lobule of the human ear. External ear in pocket gophers covered with short fine hairs, but no appreciable fringe around margin.

Cheek pouches are found in a number of mammals, but they have been evidently developed independently even in the Order Rodentia. The pouches which have given the common designations to both pocket gophers and pocket mice, although evidently homologous between these groups, are quite different from those of other mammals. In *Cricetus* (Parsons, 1896) and *Citellus* (Sleggs, 1926), as in the catarrhine monkeys, the pouch is internal to *M. orbicularis oris*, developed in *M. buccinator*, deep to *M. platysma*; lining histologically similar to oral mucous membrane, without hair follicles, epithelium delicate and soft. The cheek pouches of pocket gophers and pocket mice are lateral to the orbicularis and buccinator muscles, lateral to the deep layer of *M. platysma*; epithelium, from gross examination, like that of the body; pouches often pigmented near the orifice, lined with short fine hairs.

Pouch opening oblique, roughly semicircular, running from near level of upper incisor to angle of jaw; pouches extensive, reaching back to shoulder, capable of considerable distention. Both pouches together are capable of holding food material almost equal in bulk to the size of the head.

Fore and hind limbs short, stout; proximal parts included in body skin. Front feet large, armed with long claws. The claws are largest in *Geomys*; in a large male specimen that of the middle digit measured 20.3 mm. long from base to tip, not allowing for curvature, and 4.7 mm. deep at base. Smallest claw of manus, that of the pollex, 5 mm. long, 1.8 mm. deep. Fourth claw somewhat larger than second. In *Thomomys bulbivorus*, of approximately the same body size, claw of third digit only 12 mm. long, 2 mm. deep. Claw of the pollex about same size as that of *Geomys*; second and fourth digits and claws subequal. In *Thomomys* the claws, besides being weaker and shorter, are more nearly straight. In both genera the claw of the pollex is like that of the fifth digit, and not at all nail-like.

In *Aplodontia* and *Citellus* the claws are specialized for digging purposes, but not to the same degree as in pocket gophers. In these two animals the pollex bears a nail, as in *Sciurus* and in a number of muroid forms.

In pocket gophers, pollex little separated from other digits. Almost opposable in *Aplodontia* but size small. In most muroid forms and in some squirrels it is a mere vestige, but its position is indicative of an ancient opposable condition such as Matthew (1904) considered primitive.

All digits short, but metacarpus long; manus, as a whole, long and narrow. Volar surface of manus covered by thick, irregularly wrinkled skin. Apical pads (Whipple, 1904) present on each digit, but poorly marked. Interdigital pads usually lacking. Two carpal pads, large, almost conjoined; thenar pad larger than hypothenar. Thenar pad covers most of falciform bone; hypothenar lies over ends of falciform and pisiform. The two pads together form the large "heel" of the front foot. Most of the weight is placed on this "heel" in

walking, so that it acts as a protection for the claws; it is used in place of an opposable digit in actions of prehension such as are involved in filling the cheek pouches; and it aids in pushing earth from one place to another and in tamping loose earth in the burrow-plug and elsewhere.

Hind feet less specialized than front; digits more nearly subequal, although middle digit longest and fifth smallest. Claws short, somewhat cone-shaped. Pocket gophers are plantigrade, as are many rodents; the foot is not lengthened, retaining the primitive proportions. Plantar surface bare; skin of sole thick and smooth. In *Thomomys*, plantar pads are vestigial, but there are apical pads at the tip of each digit and four small interdigital pads between the bases of the toes. The metatarsal pads consist of a thenar, at the base of the hallux, and a large hypothenar pad at the base of the fifth digit. The latter pad is more distal than the thenar eminence. The planta is smooth compared with that of other rodents. *Geomys* has lost all but the apical pads; the sole is smooth, with a few irregular, rounded wrinkles. *Aplo dontia*, although also fossorial, exhibits the typical plantar pads, all well developed.

Tail shorter than body; relative length different, however, in different species and different individuals. Proximal three-quarters of tail quadrate rather than terete; near tip, however, it becomes rounded. Hairs on tail short; in some individuals, last half of tail nearly naked. Skin irregularly wrinkled, with numerous small papillae. Tip blunt and rounded, swollen looking. Merriam (1895) concluded that the end of the tail was highly sensitive. The pocket gopher, while retrograding, arches the tail so that the tip is directed downwards and almost, or quite, in contact with the substratum. Since the animal is able to travel as rapidly "in reverse" as forward, a sensitive tail is of importance. The end of the tail is highly vascular, and there are large nerves from that region.

The perineal region will be described in connection with the urogenital system.

### SKELETAL SYSTEM

Besides skeletons of *Thomomys bottae*, *Thomomys bulbivorus*, *Geomys bursarius*, *Cratogeomys castanops*, *Sciurus griseus*, *Citellus richardsonii*, *Aplo dontia rufa*, and *Neotoma fuscipes* listed in the introduction, skeletons of the following rodents were examined.

*Geomys arenarius* Merriam, Otero County, New Mexico, one.

*Perognathus fallax* Merriam, La Jolla, San Diego County, California, one.

*Perognathus spinatus* Merriam, Picacho, Imperial County, California, one.

*Ondatra zibethica* (Linnaeus), Topaz, Mono County, California, two.

*Microtus californicus* (Peale), Berkeley, Alameda County, California, one.

*Peromyscus californicus* (Gambel), Berkeley, Alameda County, California, one.

*Citellus beringensis* (Merriam), Point Hope, Alaska, one.

*Sciurus douglasii* Bachman, Placer County, California, one.

*Castor canadensis* Kuhl, Merced County, California, one.

These skeletons are in the collection of the Museum of Vertebrate Zoölogy, University of California.

## VERTEBRAL COLUMN

In pocket gophers the vertebral column is short in craniocaudal axis when compared with more generalized forms such as *Citellus* and *Neotoma*. This is evinced particularly in the cervical segment, but it is also true of the entire spine. The cervical segment is almost straight; in the normal position of the body its axis makes an angle of approximately ten degrees with the horizontal. The thoracic region is strongly curved; a line joining the centra of the third and ninth thoracic vertebrae makes an angle with the horizontal of some fifty-five degrees. Caudal to the ninth thoracic the curvature is less pronounced.

*Cervical vertebrae*.—In *Thomomys* and *Geomys* the proportion of the vertebral column represented by the cervical segment is about 16 per cent of the presacral length, 18 per cent of the thoracolumbar length; in these genera the cervical vertebrae remain discrete. In *Cratogeomys* (two old specimens) some cervical vertebrae fuse, although the proportion of cervical to thoracolumbar segments, 17 per cent, is greater than that which Hatt (1932) considers critical for ankylosis. The last six cervical vertebrae are bound together by ligaments and by a dovetailing of both centra and lamina with the result that they are almost immovable.

*Atlas*.—Roughly ovoid, transverse axis the longer; ventral arch, narrower and shorter than dorsal, bears small ventral (anterior) tubercle. Dorsal arch convex in both transverse and longitudinal axes, bears small dorsal (posterior) tubercle; cephalic margin frequently, and caudal margin regularly, indented; spine of epistropheus fits into notch of latter; dorsal arch pierced near laterocranial angle by small atlantal foramen for first spinal nerve. Groove for ventral ramus of this nerve runs ventrad from atlantal foramen. There may be a foramen for this nerve in transverse process.

Cranial articulating surfaces large, elongate dorsoventrally, relatively shallow compared with those in other rodents. Caudal articulating facets almost round, slightly concave. Dorsal to each caudal facet a deep groove for vertebral artery and second spinal nerve. In other rodents, including the heteromyine forms, the vertebral artery appears to pass through the atlantal foramen, as it does in most other mammals.

"Wings" of atlas small as in most rodents; dorsal part almost at right angles to ventral part; foramen transversarium vestigial, since vertebral artery does not traverse it.

*Epistropheus*.—Dens short, bluntly rounded. Cranial articular surfaces of axis roughly triangular and convex; spine nearly vertical, relatively larger than in other rodents. In *Cratogeomys* the spinous process may fuse with that of the third vertebra, and the body of axis overlaps that vertebra ventrally. Vertebral foramen large; centrum nearly flat dorsally; transverse process little more than a V-shaped arch around vertebral artery, directed caudodorsad and laterad.

The remaining cervical vertebrae are much alike. Bodies elongate in transverse axis and short in other two axes; cranial surfaces concave transversely; caudal surfaces convex; dorsal surfaces of bodies, forming floor of vertebral canal, increase in convexity caudad with the result that the vertebral foramina are kidney-shaped. Spinous processes, except that of third cervical, minute; transverse processes, in third cervical oblique, become transverse in sixth; dorsal and ventral tubercles of transverse processes poorly differentiated except on sixth cervical where ventral, or carotid tubercle, is distinct. This process is large and caudally directed in *Thomomys* and *Geomys*, much smaller in *Cratogeomys*. Foramina transversaria large in middle five cervical vertebrae, but absent or vestigial in seventh. The loss of this foramen in the seventh cervical is probably a result of a complete fusion of costal and transverse elements; in a specimen of *Geomys* it was present on one side, and on the other side there was merely an indentation in the same position. Cranial articular processes (prezygapophyses) large, project forward from cranial margin of dorsal arch, leaving rectangular incisure between them. Caudal processes not distinct from the arch; they are areas of the arch facing ventrad and covered with articular cartilage.

*Thoracic vertebrae*.—The thoracolumbar region of the vertebral column varies in number of vertebrae from eighteen to twenty, usually nineteen. Most specimens exhibit twelve thoracics, but nearly a fifth have thirteen. Lumbar vertebrae usually seven; in about one-third of specimens only six. No correlation in number of thoracic and lumbar vertebrae; twelve and seven, twelve and six, thirteen and seven, thirteen and six, all occur. There is a general tendency in mammals to reduce the number of segments bearing ribs, so it seems probable that the more primitive number of thoracic vertebrae is thirteen (cf. Howell, 1932) rather than twelve. The variation in number of thoracic vertebrae in pocket gophers is partly atavistic, if this conclusion be correct.

First thoracic vertebra, and to lesser degree second, similar to cervicals. Cranial surface, however, nearly flat, whereas caudal surface concave. Bodies of first two thoracic vertebrae longer than those of cervicals; this tendency is progressive throughout the thoracic series. Centra increase in width from seventh to twelfth. Vertebral foramina suffer progressive reduction from first to fifth, but caudal to eighth, canal formed by these foramina begins to enlarge to accommodate lumbar enlargement of spinal medulla. Spinous processes poorly developed on cranial thoracic vertebrae, but increase in height to the ninth; caudal to this, height decreases but longitudinal axis increases. First three spines nearly perpendicular to bodies of their vertebrae, but next six inclined increasingly in a caudal direction; change in inclination of spines from caudal to cranial occurs about eleventh thoracic vertebrae. Hatt (1932) considers that the spines of the thoracic vertebrae in pocket mice and kangaroo rats show phylogenetic influences rather than adaptational ones, and these processes are similar to those of pocket gophers. While *Microtus* and *Ondatra* agree in this feature with the geomyoid forms, the spinous processes in the thoracic region of *Rattus* and *Neotoma* are quite different. In these rodents the second thoracic spine is elongate, and the rest are more erect than in the other species.

Transverse processes, caudal to third thoracic, divided into dorsal and ventral elements; latter articulate with tubercles of ribs, whereas dorsal processes serve for muscle attachments. Dorsal elements tend to further divide, beginning at sixth or seventh thoracic, into cranial mamillary processes (metapophyses) and caudal accessory processes (anapophyses); differentiation complete in tenth or eleventh thoracic vertebra.

Articular processes of first two thoracic vertebrae similar to those of cervicals. From third to sixth thoracic, cranial articular surfaces face dorsolaterad and represent two segments of circle. Caudal articulating surfaces reciprocal to cranial ones. In last two or three thoracic vertebrae, cranial articular processes are groovelike, facing mediad; caudal processes are tonguelike, fitting into the grooves—a strong joint, yet permitting a certain amount of motion. Similar joints are present in certain artiodactyls, and many mammals show a tendency in this direction.

Cranial costal pits (facets) present on seventh cervical vertebra and on all except last thoracic, articulate with capitula of ribs. Caudal and transverse costal pits present on each thoracic vertebra.

*Lumbar vertebrae*.—Usually seven in pocket gophers, but may be only six. Stouter and longer than thoracics. A medial ventral ridge present on each, developed in response to the psoas muscles. Vertebral canal decreases in size from beginning of lumbar series to the end; spinous processes increase in height; articular processes are like those of last thoracic; transverse processes (diapophyses), which appear to represent fused ribs, vestigial on first lumbar, increase to sixth lumbar vertebra, then decrease slightly.

*Sacral vertebrae*.—Typically five sacral vertebrae in pocket gophers; in old specimens there may be six; last lumbar or first caudal taken into sacral complex. Individuals may exhibit asymmetry in fusion of last transverse process, and, although the spinous processes may be fused, the rest of the vertebra may be free. There are five sacral vertebrae in *Aplodontia*; four in *Neotoma*, in *Ondatra*, in *Microtus*, and in *Castor*; and three in squirrels. In adult pocket gophers, bodies usually solidly united but identities retained. First sacral vertebra about size of last lumbar, second slightly smaller, and remaining three progressively more like caudal vertebrae in size. Vertebral canal much reduced in sacrum; spines higher than those of thoracic or lumbar regions, usually ankylosed together; cranial articular



processes of first sacral like those of lumbar; both cranial and caudal articulating processes vestigial, separate structures being represented by ridges; transverse processes fused together to form lateral masses of sacrum, leaving small sacral foramina between them.

Ilium solidly united to first two or three sacral vertebrae. A bony bridge in *Geomys* is developed between spine of ischium and last sacral transverse process. In *Thomomys* a ligament and muscle fibers are found here; the bridge is formed apparently by laying down bony substance in the ligament. A similar connection between ischium and sacrum is present in the sloths and armadillos and in certain bats (Kingsley, 1925), whether developed in this manner or not.

Sacrum arched on pelvic surface, this more pronounced in females than in males.

*Caudal vertebrae*.—Number, in five skeletons in which the tail was complete, either sixteen or seventeen, exclusive of any fused with sacra. First few are short, length increasing gradually to sixth or seventh, then decreasing; vertebral canal (and neural arches) incomplete, caudal to third or fourth; vestigial spines on each complete neural arch; cranial articular processes on first twelve caudals, these minute after first two; caudal articular processes on only two or three vertebrae. Chevron bones between vertebrae on ventral side except at distal extremity of tail; they do not form arches as in squirrels, but are flat and roughly M-shaped, much as in *Onychomys*. Near distal end of tail these bones become paired and rounded, or ovoid.

#### STERNUM

In pocket gophers the sternum consists of manubrium, four (rarely five) segments or sternebrae and xiphisternum. These six elements appear to be typical of rodents; all genera examined exhibit that number. Other mammals may have more, and in pocket gophers there is an occasional intercalary bone between the last sternebra and the xiphisternum. This extra segment may be double or single, or present on one side only. In pocket gophers at birth the sternum is poorly ossified; there are two centers in manubrium, two in xiphisternum, and two in each of the first three sternebrae.

In old specimens, particularly in *Geomys*, there is a keel, increasing the area of attachment of the pectoral muscles; in that genus the dorsoventral axis of the sternum is greater than those in the other two genera.

Manubrium sterni roughly triangular, with a truncate, caudally directed apex, and emarginate sides. In *Geomys* and *Thomomys*, jugular notch poorly developed and cranial margin nearly straight; in *Cratogeomys*, notch well marked; manubrium wide. Clavicular facets indent the craniolateral angles; precise positions vary individually, but they are more cranial in *Geomys* than in other pocket gophers. Roughened pit for first costal cartilage on lateral margin, caudal to clavicular facet. On caudolateral angle a smaller pit for second cartilage. The manubrium in the muroid forms examined is similar to that in pocket gophers, but in the squirrels and *Aplodontia* it is diamond-shaped, with a strong keel.

Four sternebrae alike, except in a specimen of *Geomys* where last is double; roughly rectangular; decrease in length from first to fourth. When intercalary element is present, it is the shortest.

Xiphisternum elongate, slender and shallow compared with sternebrae; expands distally, continuous with large heart-shaped cartilage. Articulates with last sternebra, forming angle with it of about 190 degrees; directed ventrocaudad.

## RIBS

In pocket gophers there are twelve or thirteen ribs. All are double-headed except last; capitulum articulates with centrum, tuberculum articulates with the transverse process. Heads tend to unite as transverse processes are reduced progressively caudad.

First rib stouter than others; neck long; body nearly at right angles to neck; tuberculum large, articulates with transverse processes of seventh cervical and first thoracic. Fourth to tenth ribs with angles well marked and produced; *M. serratus posterior superior* attaches to these ribs and is probably responsible for development of angles. All ribs bear costal cartilages; those of first seven reach sternum; next four cartilages articulate with last costosternal cartilage; last one or two free. Costal grooves poorly marked except in old animals.

There are twelve ribs in squirrels; thirteen in *Aplodontia* and the muroids.

## SKULL

The anatomy of the skull in pocket gophers has been exhaustively described by Merriam (1895) and the cranial foramina are described in a separate paper (Hill, 1935b).

## APPENDICULAR SKELETON

The skeletal parts of the appendages reflect, in a large measure, the influence of "habitus." That "habitus" is not entirely responsible for the shape of the limb bones, however, is indicated by the differences exhibited by bones of fossorial mammals, such as the pocket gophers and *Aplodontia*. Also the great similarity between the bones of ground and tree squirrels indicates that "heritage" plays an important part in shaping the skeleton.

*Pectoral limb and girdle*

*Scapula* (fig. 1).—In pocket gophers irregularly triangular; vertebral border nearly straight, also axillary border, except the irregularity near the caudal angle caused by the fossa for teres major. This angle, in *Thomomys bulbivorus*, nearly a right angle (excluding irregularity); somewhat less than this in *Geomys*; in *Cratogeomys* and *Thomomys bottae* approximately 60 degrees. The magnitude of the caudal angle is inversely proportionate to the ratio of width to length in the scapulae of these species. Cranial angle rounded. In *Thomomys bottae* it is largely because of the development of this region that the scapula is wide, but in *Cratogeomys* the entire scapula is broadened. Cranial border emarginate, with extensive suprascapular notch.

In half-grown specimens of *Thomomys* the coracoid is free; in pocket gophers it shows no indication of two centers, as Howes (1893) reported in other rodents and as found in a young specimen of *Aplodontia*. Large coracoid strongly curved ventromedially; large supra-glenoid tuberosity projects laterad from base of coracoid.

Glenoid fossa ovoid, elongate in cranio-caudal axis. Coracoid element forms cranial third (or thereabouts) of fossa; curves ventrad, clasping cranial part of head of humerus. Infra-glenoid tuberosity irregular, continuous dorsally with axillary ridge.

In *Thomomys*, the fossa for teres major is relatively small, largely caudal; consists of excavated area in axillary border, near caudal angle. Larger in *Geomys bursarius*; still larger

and more laterally directed in *Cratogeomys*. In *Geomys arenarius*, it forms a third fossa on lateral surface of scapula, separated from infraspinous fossa by axillary ridge.

Vertebral border thickened, probably in response to stout serratus anterior, levator scapulae, and rhomboideus muscles.

Costal surface of scapula slightly concave, fitting curvature of thorax. Opposite the spine a deep groove and, on either side of this, weak ridges. A larger ridge separates teres major fossa from subscapular.

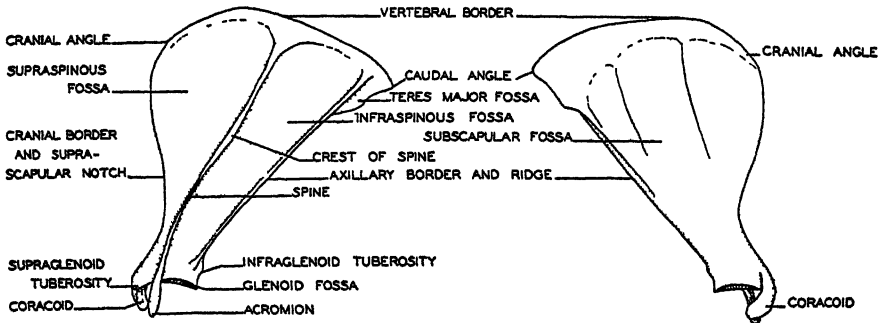


Fig. 1. Scapula (*Thomomys bulbivorus*). Slightly larger than natural size. Left, lateral view. Right, medial view.

Lateral surface divided by spine of scapula into supra- and infraspinous fossae. The former is larger dorsally, but much reduced near glenoid angle by suprascapular notch. Infraspinous fossa narrow, elongate, regular, and deep. Supraspinous fossa narrower in specimens of *Geomys bursarius* and *Cratogeomys* than in other pocket gophers. Spine high, nearly straight and nearly perpendicular to surface of scapula; in *Thomomys*, crest situated approximately midway between vertebral border and acromion. Within a genus the height of the spine seems to be more or less inversely proportionate to the width of the scapula, but in *Cratogeomys* the spine is relatively the highest and the scapula is relatively the widest of the three genera. The spine probably reflects the relative development of the suprascapular muscles, which arise from its sides.

Acromion long and narrow, approximately a third the length of the scapula; metacromion process vestigial or absent. Tip of acromion attached to clavicle by ligaments.

Measurements (see table 1, p. 101) show that the forelimb is shortened in the fossorial types, with a less important increase in the length of the scapula. The spine is higher in the fossorial types than in other rodents, indicating an enlargement of the suprascapular group of muscles.

The coracoid is larger in pocket gophers than in other rodents, probably because in the former *M. pectoralis minor* is inserted on it. The absence of the metacromion in these rodents may be a result of migration of the insertion of *M. omocervicalis* to the clavicle. In the heteromyine forms the metaacromion process is present, though poorly developed; it is large in *Apodontia*, squirrels, and wood rat; but absent in *Castor* and the *Microtinae*.

As Tullberg (1896) remarked, the scapula in *Apodontia* resembles closely that in the squirrels; size is the only constant difference.

**Clavícula.**—Of moderate size in pocket gophers; sternal end enlarged and round in section, acromial end flattened and widened. Lateral extremity curved ventrad. No true acromioclavicular joint, but stout tendon attaches to acromion. Sternal end articulates with cranio-lateral angle and cranial surface of manubrium sterni. A small articular cartilage in the joint is usual. Acromioclavicular ligament roughens lateral end, and stout coracoclavicular ligament attaches to sunken line on caudoventral surface.

**Humerus** (fig. 2).—In pocket gophers short and stout; muscular processes well developed. Head large, rounded, set at angle of about 130 degrees to the shaft. Neck reduced to groove between tubercles and head, a deeper notch caudally. Greater tubercle large, with three

depressions: tendon of supraspinatus inserts into most cranial one; tendon of infraspinatus inserts into middle, largest depression; tendon of teres minor inserts into most caudolateral, smallest depression. Distad and caudad, between tubercle and head of the humerus, a roughened fossa from which lateral head of *M. triceps* takes origin. Lateral base of greater tubercle is excavated, giving origin to fibers of *M. brachialis*.

Intertubercular sulcus, in which tendon of long biceps muscle lies, deeper in pocket gophers than in most rodents. Lesser tubercle about one-third as large as greater, bears single impression for subscapularis tendon. The shaft of the humerus would be slender were it not for strong muscle ridges, and the bone is easily fractured. The weakest point is just distal to the lateral ridge. This ridge is more strongly developed than in the other rodents examined. Extends from greater tubercle half to two-thirds of distance to condyle. In *Thomomys bulbiworius* the highest part of the lateral ridge is nearer the head of the humerus than in the other species of pocket gophers (see table 1). Apex bent laterocaudad; entire ridge directed away from pull of pectoral muscles. This is probably the chief element involved in the development of the ridge, and the insertions of the tendons are marked by a narrow sunken line along the cranial side of the ridge. The deltoid is less important, but it doubtless aids the pectoral group.

Medial ridge distinct but poorly developed; continues from lesser tubercle distad to medial epicondyle. Insertions of teres major and latissimus dorsi tendons marked by sunken or roughened area distal to lesser tubercle. Rest of medial ridge poorly marked. Lateral epicondylar ridge begins on caudal side of shaft near insertions of teres major and latissimus dorsi; runs obliquely laterodistad, becoming stronger towards epicondyle, curving cranial near that process. Lateral epicondyle scarcely separable from ridge, but thicker.

Medial epicondyle short, blunt, projecting from medial mass nearly at right angles to axis of humerus. Excavated on proximal side for insertion of long coracobrachial muscle. In pocket gophers no medial epicondylar ridge or entepicondylar foramen is present.

Condyles poorly separable into large, medial trochlea and smaller, indistinct capitulum; differentiation least evident in *Thomomys* and most complete in *Cratogeomys*. Capitulum restricted to cranial surface; articulates with head of radius. Trochlea wider caudally; articulates with semilunar notch of ulna. Central groove of trochlea shallow and broad; medial flange not sharply inclined. Olecranon and coronoid fossae deep, rarely breaking through above trochlea.

The humerus is shortest in *Cratogeomys* and *Geomys*, longest in *Thomomys bulbiworius* (see table 1). There is a similar relation between the absolute humeral measurements in animals of approximately similar sizes. The width across the epicondyles is greater in pocket gophers than in most other rodents (see table 1).

The humerus in *Ondatra* is very similar to that in pocket gophers in general proportions, in ridging, and in appearance; but the capitulum is less distinct. In *Neotoma*, in specimens without the entepicondylar foramen, the humerus is more elongate, slender, and relatively narrow across the epicondyles. In *Citellus* and *Aplodontia*, the humerus is much alike; entepicondylar foramen large; pectoral and deltoid insertions on lateral ridge forming elongate, V-shaped marks; sulcus of trochlea deep and its medial lip steep; humerus short, with strong attachments for muscles. The entepicondylar foramen is present in pocket mice and in most muroid forms; it is absent in the Microtinae, but present in most cricetine species. In *Neotoma* it is present in almost half of the specimens (cf. Howell, 1926).

*Radius and Ulna* (fig. 3).—In pocket gophers the radius and ulna have only a limited amount of independent motion. Proximal tenth and distal third of radius pressed to ulna and bound to it by ligaments. However, in feeding and placing food into the cheek pouches there must be supination to an appreciable degree.

Olecranon long, giving larger area for insertion and greater leverage for *M. triceps*; caudal end curved mediad, roughened for insertion of triceps. Relatively short in *Thomomys bulbiworius* (see table 1), less rugose than in other pocket gophers.

Semilunar notch relatively deep and semicircular; radial facet on cranio-lateral side receives head of radius. Coronoid process, on craniodistal margin of semilunar notch, projects mediad as well as cranial.

Roughened tuberosity of ulna is distal to coronoid process. Body of ulna excavated on lateral side forming a lateral fossa. The ridge on the caudal margin of this fossa probably represents the "dorsal border of the ulna" of human anatomy. Sunken line in distal third of ulna, cranial to this ridge, marks attachment of long part of radial collateral ligament. This ligament is stout; it probably opposes the component of force that would tend to twist the ulna in the elbow joint when the flexor mass of the forearm contracts (cf. Holliger, 1916).

Distal end of ulna exhibits two grooves; one, on dorsal surface between radius and ulna, permits passage of most of extensor tendons; the groove on the ulnar side contains tendon

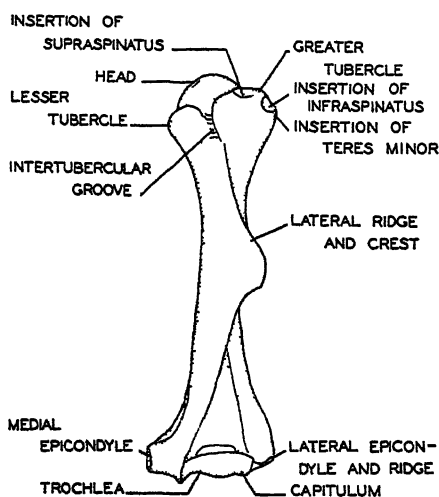


Fig. 2. Humerus (*Thomomys bulbivorus*), cranial view,  $\times 1\frac{1}{2}$ .

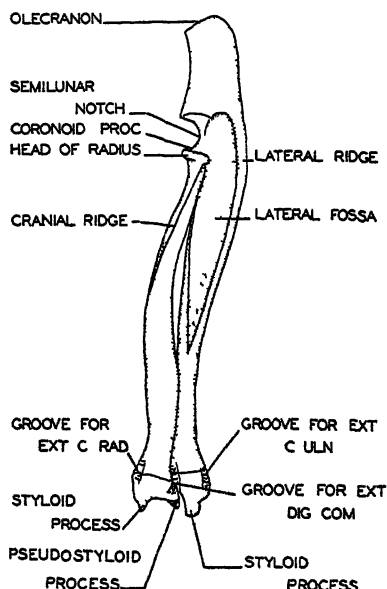


Fig. 3. Radius and Ulna (*Thomomys bulbivorus*), lateral view,  $\times 1\frac{1}{2}$ .

of *M. extensor ulnaris*. Styloid process rounded; fits into rounded depression between triquetrum and pisiform bones. This type of articulation is found in all the rodents examined.

In pocket gophers the radius is much more rugose than in more generalized rodents. In *Cratogeomys* the radius is relatively longer than in the other genera of pocket gophers (see table 1).

Head of radius ovoid in pocket gophers—probably indicative of reduced independence of motion (cf. Holliger, 1916); it is irregularly rounded in *Sciurus*, less rounded in *Citellus*. In some specimens, groove on lateral side of radius articulates with small ridge on ulna; this reduces movability of radio-ulnar joint. Neck of radius attaches to ulna by ligaments. Oblique part of cranial border extends from lateral side of head to middle of radius. Slight groove on lateral surface, several millimeters distal to oblique line, for tendon of *M. adductor pollicis longus*; tendon runs in a spiral over cranial border, bridged by stout ligament. Another groove present on radial "malleolus" for this tendon.

In pocket gophers, tuberosity of radius poorly marked; situated on medial side near head. Pronator ridge extends obliquely laterodistad from tuberosity; in some specimens unites distally with cranial border.

In pocket gophers and pocket mice, distal end of radius on ulnar side simulates styloid process. This "pseudostyloid process" is slightly smaller than true styloid process; rounded, situated on volar side, does not appear in dorsal view of articulated foot. Styloid process of radius articulates with depression in scapholunar bone. Carpal surface of distal end of

radius otherwise concave. Volar surface also concave, forming groove for flexor tendons. Groove on ulnar side of dorsal surface, with similar concavity in ulna, forms compartment for tendons of extensor muscles.

The radius in *Aploodontia* and *Citellus* is irregular, as in pocket gophers, but the pseudostyloid process is absent. In most other rodents the radius is longer and smoother, without crests and roughened areas for muscle attachments; rounded in cross section, rather than roughly triangular.

*Carpus* (fig. 4).—The relationships of the bones of carpus and metacarpus are indicated in the accompanying diagram, which is equally valid for the three genera of pocket gophers. The shape of the various bones is relatively constant.

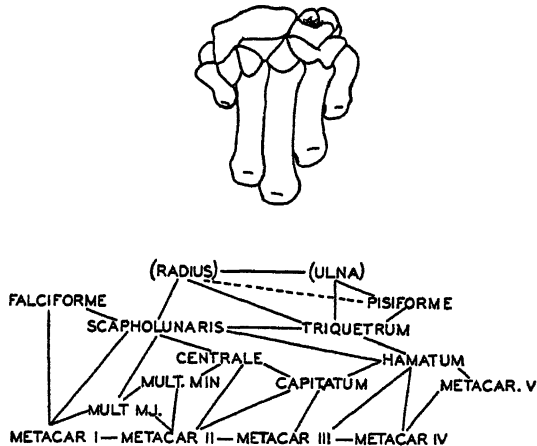


Fig. 4. Carpus and metacarpus (*Thomomys bulbivorus*),  $\times 2$ , with schema to show articulations (represented by solid lines; broken line indicates articulation when manus flexed).

*Os scapholunaris*.—Represents fused navicular (scaphoid or radiale) and lunate (lunar or intermedium) bones, characteristic of rodents, as of modern carnivores. In rodents, centrale usually distinct. Proximal surface rounded; a rounded depression on radial side for styloid process of radius; a rounded process on radial side articulates with falciform and greater multangular. Distal surface concave; a small process at volo-ulnar angle articulates with hamate.

*Os triquetrum* (cuneiform or ulnare).—Irregularly triangular in dorsal and proximal views. Rounded depression, into which styloid process of ulna fits, occupies most of proximal surface. Entire volar surface articulates with pisiform, which completes fossa for styloid process of ulna. Radial surface flat, distal surface with rounded keel fitting into groove in hamate. Pseudostyloid process of radius articulates with triquetrum when manus is flexed.

*Os pisiforme*.—This bone has been considered a sesamoid, but its constant presence in mammals and large size in many forms make this improbable. A recent theory proposed by Gillies (1929) is that the pisiform is a displaced member of the centrale series. This author presents some reasonable arguments to support his thesis. In pocket gophers, pisiform relatively large, projecting towards volar side of manus, covered by hypothenar carpal pad. In *Ondatra* and *Citellus* the pisiform articulates with the scapholunar; in pocket gophers it is excluded by the pseudostyloid process of the radius from this bone.

*Os falciforme*.—Usually considered a sesamoid, although von Bardeleben (1894) concluded that it represented the prepollex. Well developed in pocket gophers and indeed in other rodents; projects in volar direction; united to pisiform by strong ligament, two bones forming an arch below flexor tendons. Volar end swollen and irregular, covered by thenar carpal pad. Of less dense bone than other carpal elements.

*Os centrale*.—In pocket gophers second smallest bone in carpus. Triangular, apical angle almost 90 degrees and directed distad. Base wide and slightly convex, fitting into concavity of scapholunar. Radial and ulnar sides of triangle approximately equal. Does not reach volar surface of manus. In *Ondatra*, centale flat and wide, articulating with four distal carpal bones, but in *Citellus* and in *Aplodontia* more like that in pocket gophers.

The four distal carpal elements probably represent the first four carpalia of lower vertebrates, according to Broom (1921).

*Os multangulum majus* (trapezium or first carpal).—In most rodents the larger of the first two carpals; roughly trapezoidal in dorsal view, nearly triangular in volar aspect.

*Os multangulum minus* (trapezoid or second carpal).—Small, tapering toward volar end, triangular in dorsal view. Lies in deep groove on proximal surface of second metacarpal; does not reach volar surface of carpus. Proximal surface convex; articulates with centrale. Second metacarpal excludes from articulation with capitata.

*Os capitatum* (magnum or third carpal).—Slightly larger than either of first two carpals. From dorsal aspect roughly pentagonal. Reaches volar aspect of manus; this part large and rounded.

*Os hamatum* (unciform or fourth carpal).—In rodents, and in most mammals other than primates, the clawlike process from which this bone derives its name is absent. In pocket gophers it is like a wide and thick set-square in shape; the right angle directed distad between third and fourth metacarpals. Deep groove in proximal surface articulates with keel of triquetrum. Small crescentic part appears on volar aspect of manus. In squirrels and in *Aplodontia*, the hamate is much as in carnivores, with proximal surface convex, distal surface nearly flat; in *Ondatra* it is more like that in pocket gophers.

*Metacarpus* (fig. 4).—First metacarpal short, on same level as distal carpal row. Fifth metacarpal likewise short, situated proximally; articulates with lateral surface of hamate. Third metacarpal longest; second and fourth noticeably longer than first and fifth. Proximally the metacarpals are irregular, articulating with distal carpal elements, and are closely adpressed. Heads expanded and large. A pair of sesamoid bones present at each metacarpophalangeal joint, including that of the pollex. Keels on volar side of metacarpal heads well developed, more rounded than in some mammals.

*Phalanges*.—First two phalanges of each digit short and stout, especially in middle three digits. In pocket gophers, ungual phalanx of third digit longest, bears largest claw. Relative disproportion between claws of third and of other two inside digits greatest in *Geomys*, least in *Thomomys*; this reflected in relative sizes of ungual phalanges. In other rodents, the proximal two phalanges are more elongate than in pocket gophers.

### *Pelvic limb and girdle*

*Os coxae* (figs. 5, 6).—Long and narrow in pocket gophers, with muscular processes strongly developed. Sacroiliac joint solid, attaches to two or three sacral vertebrae. In *Geomys*, besides sacroiliac joint, ischium also attaches to vertebral column; union involves fifth sacral vertebra, sometimes fourth also. Both ilium and ischium, especially the latter, are relatively long in the pocket gophers (see table 1), in relation to body length and to free limb length. The hip bone in female specimens is relatively longer than in males.

In male pocket gophers and in some females, coxal bones united by slender symphysis; in other females (cf. Chapman, 1919), symphysis absent. Hisaw (1924, 1925) showed that the symphysis is resorbed under the influence of an ovarian hormone, and that at sexual maturity the females begin to lose the symphyseal bar. The symphysis is near the caudal end of the ventral border of the hip bone, and from its position might be thought to be formed from the ischium. A young specimen of *Thomomys bottae* (123 mm. total length), although it does not show clearly the suture between the ventral ramus of the ischium and the pubis, it does indicate that the entire ventral border of the hip bone is formed from the pubis. This is indicated also by conditions in a still younger animal, but it is impossible to be certain from the specimens available. In some insectivores (*Chrysochloris*, *Condylura*, *Myogale*) the pubis forms the entire ventral border of the hip bone (Leche, 1883), and in most muroid forms this

is true (Giebel, 1900). The symphysis is largest in *Sciurus*, then decreases in other forms in the following order: *Citellus*, *Dipodomys*, *Perognathus*, *Aplodontia*, *Castor*, *Neotoma*, *Onychomys*, and pocket gophers. In some of the Microtinae a symphysis is said to be absent (Chapman, 1919).

Acetabulum situated slightly caudal to middle of hip bone. Deeper in pocket gophers than in other rodents; hip joint strengthened with little loss of movability. Lips of cup usually incomplete on caudoventral side where ligamentum teres attaches, bridged over by a ligament which may become ossified. Irregular cavity at "bottom" of acetabulum contains Haversian gland, generally thought to have significance in lubrication of joint.

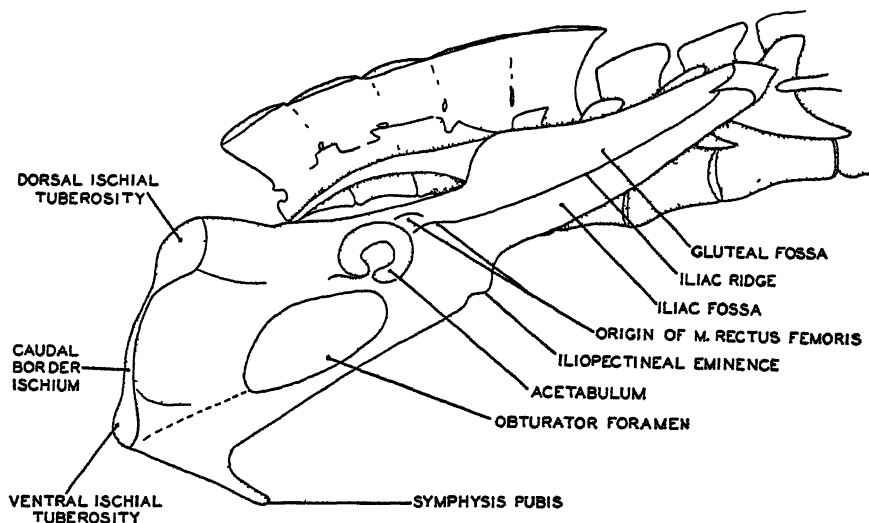


Fig. 5. Hip bone (*Thomomys bulbivorus*),  $\times 1\frac{1}{2}$ .

Obturator foramen ventral and caudal to acetabulum; in *Thomomys*, elongate oval and relatively regular, lower border less concave than dorsal, and main axis horizontal. In *Geomys* and *Cratogeomys*, cranial part of opening, transmitting obturator nerve and vessels, separated from remaining parts by bony processes or bony bridge. The obturator foramen of other rodents is relatively larger.

Ilium extends from approximate middle of acetabulum in cranial direction, elongate and prismatic. Cranial end pointed and thickened, representing crest and tubercle. Laterally the crest is produced into recurved spine, which gives origin to part of *M. gluteus medius*. Iliac ridge runs from spine to dorsocranial part of acetabulum, separating gluteal fossa from iliac fossa. On iliac ridge near acetabulum is a well-marked tubercle, from which straight head of *M. rectus femoris* arises; roughened area dorsocaudal to tubercle gives origin to reflected head of this muscle. Gluteal fossa narrow, but deeply excavate. Faint line in some specimens separates areas giving attachment to *Mm. gluteus medius* and *gluteus minimus*. In *Neotoma* and the muroids, *M. scansorius* has invaded the iliac fossa, displacing *M. iliacus* to the ventral margin and modifying the iliac ridge noticeably. In *Aplodontia*, iliac ridge is similar to that in pocket gophers, whereas in squirrels it is somewhat intermediate between geomyoid and muroid types.

Dorsal and ventral borders of ilium roughly parallel for most of lengths, although both slightly convex. Dorsal border indented near caudal end by great sciatic notch. Opposite this, ventral border is emarginate to permit *M. psoas major* to pass out from pelvis to thigh. Immediately caudal to ventral emargination, well-developed iliopectineal eminence to which tendon of *M. psoas minor* attaches. This marks approximate caudal end of ilium.

Ischium forms rest of dorsal and caudal parts of hip bone. Ischial tuberosity divided into dorsal and ventral tubercles; thickened dorsocaudal margin between these probably also represents part of ischial tuberosity of man. Dorsal tuberosity large, swollen; projects



laterad. In *Cratogeomys* it is nearer the acetabulum than in the other two genera. In *Thomomys* and *Geomys* a small shallow groove in front of tuberosity in which tendon of *M. obturator internus* lies; groove narrow and deeper in *Cratogeomys*, even in young specimens. It represents lesser sciatic notch. Ischial spine in *Thomomys* and *Cratogeomys* poorly developed, but in *Geomys* united to sacrum by bony bridge, and greater sciatic notch becomes a foramen (see fig. 6).

In male specimens descending ramus of ischium wider than in female, less laterally and caudally inclined. Caudal border thickened, epiphyseal in origin. It is more oblique in *Cratogeomys* than in the other genera of pocket gophers and more nearly straight. In *Thomo-*

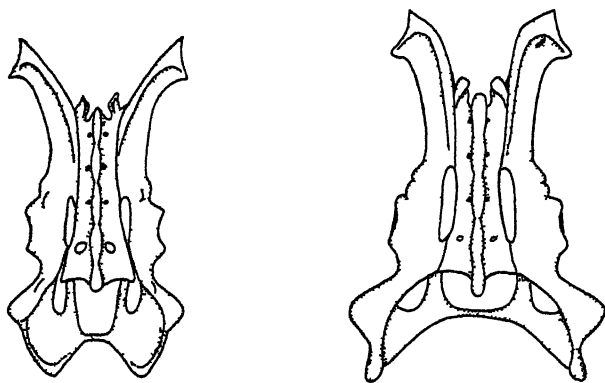


Fig. 6. Hip bones from above. Right, *Geomys bursarius*. Left, *Thomomys bottae*. Both natural size.

*mys* and in *Cratogeomys* the ventral ischial tuberosity marks probable lower limit of ischial ramus; it is somewhat more dorsal in *Geomys*.

In pocket gophers, pubis extends caudad, ventral to obturator foramen and ischium. Body of pubis small, hardly separable from ramus. A dorsally directed ramus absent. Pubis almost completely excluded from acetabulum by acetabular bone, as in other rodents. Cranial limit marked by iliopectineal eminence. Ventral border almost straight except where symphyseal region projects ventrad. In adult females, symphysis is reduced, but a vestige remains; in males a narrow bar runs ventrad and mediad to unite and fuse with one on the opposite side.

In the squirrels the ischium takes a small part in the formation of the symphysis, but in *Aplodontia* it is excluded from the symphysis, retaining, however, its normal position.

Caudal border of hip bone in pocket gophers is oblique; in most rodents nearly vertical. This obliquity increases the angle of insertion of *Mm. adductor magnus* and *semimembranosus* and would increase their power. Consequently this may be an adaptation to fossorial habits. That it is present to some degree in *Dipodomys* does not militate against this hypothesis, since these rodents are capable diggers, but it suggests that the condition may have some phylogenetic significance.

In rodents, especially in pocket gophers, sacroiliac angle is small. In the squirrels, muskrat, and meadow mouse the ilium articulates with a single vertebra; part of the second sacral vertebra enters into the joint in *Neotoma* and *Aplodontia*; two vertebrae are usually involved in *Thomomys* and *Geomys*, with rarely a part of the third; in *Cratogeomys*, usually three. A strong sacroiliac joint is considered characteristic of fossorial mammals by Chapman (1919).

The hind leg in pocket gophers is shorter in relation to the foreleg than is usual (see table 1).

*Femur* (fig. 7).—In pocket gophers relatively short, stout, and with large processes for muscle attachments. Neck forms less obtuse angle with shaft of femur than in other rodents; head faces slightly craniad, especially in *Thomomys*. The pit, to which ligamentum

teres is attached, is deep; a depression, in which the ligament lies, runs caudad. Articular surface of head hemispherical. Lip, to which capsule of hip joint attaches, sharp. Neck less constricted than in wood rats and squirrels.

Greater trochanter large. In pocket gophers it projects higher than head of femur and diverges from main axis of bone much as does the neck. Lesser trochanter large in pocket gophers, but smaller than greater trochanter; main axis almost at right angles to that of femur. Size probably correlated with importance of *Mm. psoas major* and *quadratus femoris* which insert on it. Trochanteric fossa large and irregular. Trochanteric crest in *Thomomys*

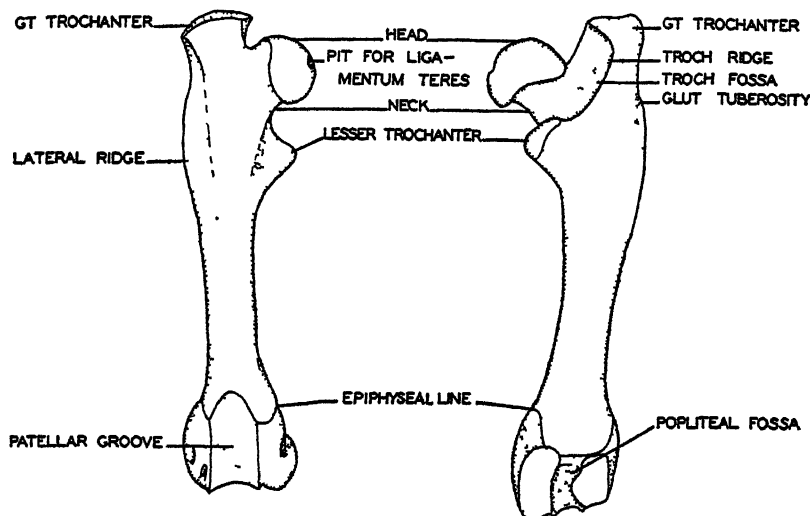


Fig. 7. Femur (*Thomomys bulbivorus*). Left, cranial view. Right, caudal view. Both  $\times 1\frac{1}{2}$ .

complete, connecting trochanters, but incomplete in individuals of other pocket gophers, as in squirrels and *Aplodontia*. No intertrochanteric line on its cranial surface. *M. vastus medialis* takes origin from cranial surface of base of lesser trochanter by tendon and fleshy fibers; tendon of *M. vastus medialis* produces deepened, roughened area on cranial surface of base of lesser trochanter—in some specimens almost a pit.

No definite third trochanter in pocket gophers and *Aplodontia*, but lateral ridge, of which it is a part, is of moderate size. Third trochanter a definite process in squirrels and heteromyine rodents, developed for insertion of *M. gluteus maximus*; also found in muroid rodents, where more distal in position. In pocket gophers, tendon of *gluteus maximus* inserts into gluteal tuberosity, a roughened area or depression at proximal end of lateral ridge of femur. Lateral ridge extends for proximal two-thirds of shaft of femur, continues into lateral epicondylar line.

There may be several sunken lines on medial surface of femur, distal to lesser trochanter, marking insertions of tendons of *Mm. iliacus*, *pectineus*, and *adductor longus*.

Proximal end of femur bent cranial; rest of shaft nearly straight. Distal end enlarged to form condyles. These are not noticeably different from those of other rodents. As in most pronograde mammals the articular surfaces are more caudal than distal in position. Medial condyle the larger; popliteal groove deep; patellar groove large and rounded.

Lateral epicondyle roughened for attachment of ligaments of knee joint and certain muscles (see fig. 8, left). Most proximal area, near caudolateral angle of distal end of femur, near epiphyseal line, gives origin to lateral head of *M. gastrocnemius* and to *M. plantaris*. Distad and cranial is a pit for fibular collateral ligament. Tendon of popliteus arises from most distal depression, near joint capsule; *M. extensor digitorum longus* takes origin from a pit between patellar groove and area of attachment of fibular collateral ligament.

Medial epicondyle smoother than lateral epicondyle (see fig. 8, right). Adductor tubercle probably represented by swollen area near epiphyseal line to which *M. caudofemoralis* attaches. Tibial collateral ligament attached to sunken area distal to origin of medial gastrocnemius muscle, but ligament and area to which it attaches much less developed than corresponding structures on lateral side of femur.

The femur is relatively shorter in pocket gophers than in other rodents compared to the length of the hip bone (see table 1).

*Patella*.—Large and elliptical. Proximal end usually slightly larger than distal.

*Tibiofibula* (fig. 9).—Tibia and fibula in pocket gophers solidly fused together; this union takes place at an early age. Distal thirds of the bones unite soon after birth and are solidly ankylosed in young of *Thomomys* of 123 mm. total length; at this age the epiphyses are still largely cartilagenous. Distal end of tibiofibula in pocket gophers exhibits fewer

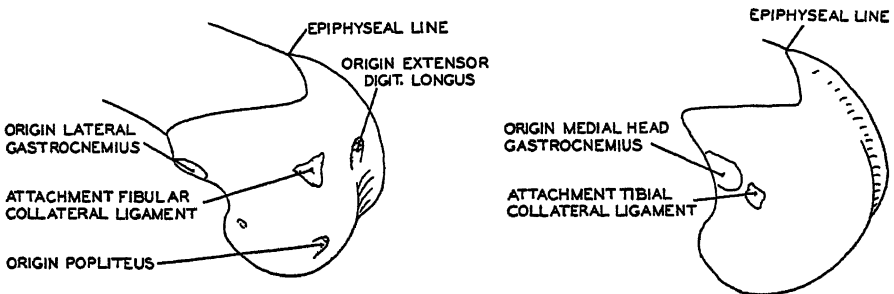


Fig. 8. Epicondyles of femur (*Thomomys talpivorus*). Left, lateral; right, medial epicondyle. Both  $\times 4$ .

traces of its compound nature than in muroid forms. Proximal two-thirds of lower leg bone divided except for head of fibula and tibia, which are solidly united. A common proximal epiphysis for tibiofibula.

Articular surfaces for femur large; medial condyle lower than lateral, concave in transverse axis and convex in craniocaudal axis. Crescentic meniscus may be partly ossified in old specimens. These ossicles apparently correspond to what Howell (1926) calls "articular sesamoids" in the wood rat. Lateral condyle higher than medial one and smaller; convex in both axes. Lateral meniscus smaller than medial.

In pocket gophers, tuberosity is part of common proximal epiphysis. Large patellar tendon inserts on tuberosity, usually leaving a deep scar. Body of tibia between proximal epiphysis and union with fibula roughly triangular in cross section, with cranial, medial, and lateral borders prominent. Cranial border or crest of tibia begins lateral to tuberosity; runs in spiral manner to cranial surface. Proximal end of crest produced laterad; crest projects over fossa on lateral surface.

*M. semimembranosus* inserts into sunken line about 3.5 mm. long, near medial border immediately distal to epiphyseal line. *M. gracilis* inserts distal to this into more irregular, slightly longer groove. Insertion of *M. semitendinosus* narrower; forms depression near cranial border midway between two ends of tibia. Triangular area between insertions of these muscles and cranial border uncovered by muscle tissue. Area of attachment of medial or tibial collateral ligament is proximal to insertion of semimembranosus.

Medial crest begins distal and caudal to medial condyle, curves mediad and slightly cranial. Becomes indistinct in distal third of leg. Proximal portion of medial crest irregular; curves over caudal fossa. Between this part of medial border and insertion of *M. semimembranosus*, an oblique fossa into which *M. popliteus* inserts. Lateral, or interosseous, border in pocket gophers a well marked ridge to which the interosseous membrane is attached.

The various crests and fossae are poorly developed in *Sciurus*; somewhat stronger in *Citellus* and *Aplodontia*, whereas in *Neotoma* and *Ondatra* they are more nearly as in pocket gophers but smaller.

Fibula separate for less than two-thirds of length. More caudal than lateral in position, relative to tibia. Head forms part of proximal epiphysis, its limits indistinguishable. Roughened area on head near epiphyseal line gives attachment to fibular collateral ligament. Body of fibula flattened on tibial and caudal surfaces. A poorly developed interosseous crest opposite that of tibia gives attachment to interosseous membrane. The fibula is rounded and skewerlike in *Sciurus*, *Aplodontia*, and *Ondatra*; it is somewhat flattened in *Citellus* and almost triangular in *Neotoma*.

Conjoined tibia and fibula in pocket gophers proximally triangular, but above malleoli, bone becomes almost round in section. Pair of ridges on laterocranial surface near malleoli,

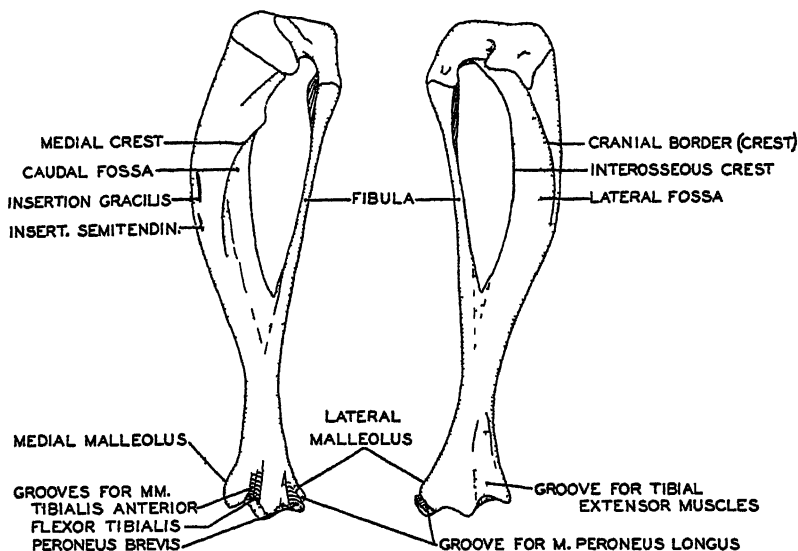


Fig. 9. Tibiofibula (*Thomomys bulbivorus*). Right, lateral view. Left, medial view. Both  $\times 1\frac{1}{2}$ .

one representing medial margin of fibula, other in line with cranial border of tibia, united by strong ligament. With the ligament they form a foramen for tendons of tibial extensor group of muscles. There are similar ridges in *Neotoma* and *Ondatra* but not in squirrels or *Aplodontia*.

Distal end of tibiofibula consists of malleoli and articular surface for talus. Lateral malleolus large, represents distal end of fibula. Oblique groove in lateral surface serves for passage of peroneus longus tendon. Tendons of other peroneal muscles pass behind malleolus in large groove, separated from groove for tendon of *M. flexor fibularis* by a ridge. The special groove in the lateral malleolus for the peroneus longus tendon is characteristic of muroid rodents (Parsons, 1896); it is poorly marked in *Neotoma*, and is absent in squirrels and *Aplodontia*.

Two grooves on cranial surface of distal end of tibiofibula: medial one for tendons of *Mm. tibialis anterior* and *extensor hallucis longus*; lateral groove for tendon of *extensor digitorum longus*. In some specimens the two grooves are united.

Medial malleolus less distinct from body of tibiofibula than lateral malleolus. In pocket gophers and in *Neotoma*, medial surface exhibits two grooves for tendons of *Mm. tibialis posterior* and *flexor tibialis*. Large groove behind medial malleolus for tendon of *M. flexor fibularis*.

Distal end of tibiofibula articulates with talus only.

Calcaneofibular ligament of ankle joint well developed. Runs obliquely caudad from cranial part of distal surface of lateral malleolus to depression on lateral surface of calcaneus. Deltoid ligament seems to correspond only to deep talotibial ligament; attaches to

medial malleolus in front of grooves for Mm. tibialis posterior and flexor tibialis, and to semicircular line on medial surface of talus. Talofibular ligament runs from medial side of lateral malleolus to lateral side of talus; not visible when ankle joint is articulated. Other ligaments of ankle joint poorly developed.

Measurements indicate that the tibiofibula is relatively shorter in pocket gophers than in other rodents of approximately the same size (see table 1).

The tarsus contains eight bones, including the medial tarsal bone.

*Talus* (astragalus).—The problem of the morphology of the talus has been reopened by Broom (1930), who considers it to represent the intermedium of reptiles rather than the intermedium and tibiale fused.

Trochlea pulleylike; medial condyle narrow, lateral one broad. Movement probably restricted to one plane. Talus broad in proportion to height, as usual in rodents. Neck short;

head large, irregularly rounded. Two facets for calcaneus: lateral one larger, strongly concave, fits dorsal process of calcaneus; smaller medial facet separated from other by a convex groove, articulating with sustentaculum tali of calcaneus. The groove gives attachment to interosseous talocalcaneal ligament.

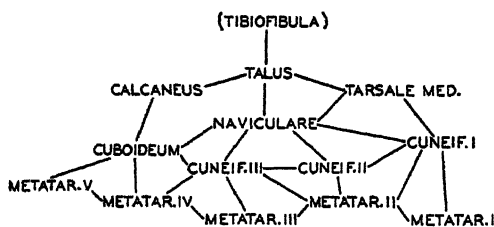


Fig. 10. Tarsus and metatarsus (*Thomomys bulbivorus*),  $\times 2$ , with schema below showing articulations (represented by lines).

*Os tarsale mediale*.—Usually considered a sesamoid, called the tarsal sesamoid bone. Von Bardeleben (1894), as with similarly placed bones in the hand, considered it a remnant of an extra digit, the prehallux. It does not appear to be an ordinary sesamoid, and von Bardeleben's thesis has not found wide acceptance, so the bone should be given a name with less prejudiced significance. I propose the designation given above as more suitable. Medial tarsal bone is roughly circular from side and flattened on medial and distal surfaces.

*Os naviculare pedis* (scaphoid).—Recently homologized with the reptilian tibiale by Broom (1930), its position is more in harmony with the older view that it represents the centrale. Proximal (caudal) surface excavate for head of talus; this surface elongate in dorso-plantar direction; otherwise not unusual.

*Ossa cuneiformes*.—In pocket gophers, first cuneiform bone is large, elongate, roughly rectangular, distally larger and more convex than proximally. Second cuneiform small, irregularly flattened from side to side, rhomboidal in dorsal aspect. Third cuneiform large, wedge-shaped as in most mammals. A process projects in plantar direction; gives attachment to ligaments and some interosseous muscles.

*Os cuboideum*.—In pocket gophers not typical; more triangular than square. Articular facet for calcaneus convex, faces lateroproximad. Distal facet for fourth metatarsal bone almost flat, slightly concave, with small lateral extension articulating with fifth metatarsal. Deep groove for tendon of *M. peroneus longus* crosses plantar surface from laterocaudal angle to mediocranial. A more irregular groove runs from dorsal surface to plantar, medial to distal articular surfaces, giving attachment to a ligament uniting cuboid to navicular and third cuneiform. In *Thomomys* and *Geomys* this groove not as marked as in *Cratogeomys*.

*Ossa metatarsales*.—The fifth is the smallest of the metatarsals. First somewhat longer, more slender, set at angle to others, perhaps as a vestige of an ancestral condition (cf. Matthew, 1904). Proximal surface of first metatarsal concavo-convex, articulating with first

TABLE 1

PROPORTIONS OF THE APPENDICULAR SKELETON IN POCKET GOPHERS AND CERTAIN OTHER RODENTS (IN PERCENTAGES)

|                                      | Width scapula <sup>2</sup><br>Length scapula <sup>1</sup> | Length scapula<br>Lengths humerus + radius | Length scapula<br>Length humerus <sup>3</sup> | Greatest width epicondyles<br>Length humerus | Length lateral crest <sup>4</sup><br>Length humerus | Length radius <sup>5</sup><br>Lengths humerus + radius | Greatest length olecranon <sup>6</sup><br>Greatest length ulna | Greatest length ischium<br>Greatest length ilium | Lengths ilium + ischium<br>Lengths femur + tibia | Length tibia <sup>7</sup><br>Length femur <sup>8</sup> | Lengths humerus + radius<br>Lengths femur + tibia |
|--------------------------------------|-----------------------------------------------------------|--------------------------------------------|-----------------------------------------------|----------------------------------------------|-----------------------------------------------------|--------------------------------------------------------|----------------------------------------------------------------|--------------------------------------------------|--------------------------------------------------|--------------------------------------------------------|---------------------------------------------------|
| <i>Thomomys bulbivorus</i> . . .     | 59                                                        | 43                                         | 80.5                                          | 32                                           | 53                                                  | 52                                                     | 22                                                             | 88                                               | 72                                               | 93.5                                                   | 85                                                |
| <i>Geomys bursarius</i> . . . . .    | 63                                                        | 48.5                                       | 90                                            | 40                                           | 63                                                  | 46                                                     | 29                                                             | 81                                               | 72                                               | 97                                                     | 82.5                                              |
| <i>Cratogeomys castanops</i> . .     | 67                                                        | 43.5                                       | 85                                            | 38                                           | 58                                                  | 49                                                     | 23.5                                                           | 80                                               | 72                                               | 97                                                     | 84.5                                              |
| <i>Citellus richardsonii</i> . . . . | 60                                                        | 43                                         | 81.5                                          | 27.5                                         | 46                                                  | 47                                                     | 17                                                             | 56.5                                             | 55                                               | 104                                                    | 75                                                |
| <i>Sciurus griseus</i> . . . . .     | 53.5                                                      | 36                                         | 72                                            | 29                                           | 42                                                  | 49.5                                                   | 16                                                             | 85                                               | 39.5                                             | 115                                                    | 66                                                |
| <i>Aplodontia rufa</i> . . . . .     | 55.5                                                      | 42                                         | 78                                            | 34                                           | 52                                                  | 46                                                     | 21.5                                                           | 78                                               | 60                                               | 104                                                    | 73                                                |
| <i>Neotoma fuscipes</i> . . . . .    | 54                                                        | 39                                         | 74                                            | 24.3                                         | 45                                                  | 47.5                                                   | 14.5                                                           | 64                                               | 56                                               | 107                                                    | 76                                                |
| <i>Ondatra zibethica</i> . . . . .   | 50.5                                                      | 43                                         | 90                                            | 33                                           | 55.5                                                | 54                                                     | 21                                                             | 92                                               | 71                                               | 136                                                    | 74                                                |

<sup>1</sup>Length scapula—glenoid fossa to vertebral border at spine. <sup>2</sup>Width scapula—cranial angle perpendicularly to axillary border. <sup>3</sup>Length humerus—most proximal surface of head to middle of trochlea. <sup>4</sup>Length lateral crest—proximal surface head of humerus to angle of crest. <sup>5</sup>Length radius—middle of capitulum to middle of distal articular surface in front. <sup>6</sup>Length olecranon—from middle of semilunar notch. <sup>7</sup>Length femur—most proximal surface of head to distal surfaces of condyles. <sup>8</sup>Length tibia—proximal surfaces of condyles to middle of distal end in front.

cuneiform and with second metatarsal. Head keeled, lateral articular mass larger than medial. Proximal end of second metatarsal narrow and squared. In *Geomys*, shaft more slender than those of the third and fourth metatarsals, but less evidently so in the other two genera. Proximal articular surfaces of third and fourth metatarsal bones face medioproximad in same oblique plane. Third metatarsal exhibits lateral process articulating with depression in fourth bone. Fifth metatarsal short and stout, with large tuberosity. Medial to this process is articular facet for cuboid. Pair of sesamoid bones at each metatarsophalangeal joint. Heads of metatarsals swollen and keeled.

*Phalanges*.—Short, less than half relative length of these bones in *Neotoma* or in squirrels.

## MUSCULAR SYSTEM

The muscular system was dissected in a number of specimens of *Thomomys bottae*, *Thomomys bulbivorus*, and *Geomys bursarius*. The following description is based on conditions found in *Thomomys*, and where differences were encountered in *Geomys* they are noted comparatively. Two specimens of *Citellus richardsonii*, one of *Sciurus griseus*, and one of *Aplodontia rufa* were also

dissected for comparison. Where published accounts were lacking in important details, a specimen of *Dipodomys spectabilis* and one each of two murid rodents (*Neotoma fuscipes* and *Rattus norvegicus*) were dissected for some determinations. Otherwise the descriptions of the muscles of rodents in Parsons (1894a, 1896), Alezais (1900), Howell (1926, 1932), and others have been used as a basis for comparison.

Individual muscles are arranged in groups on the basis of common or homologous innervation, on the evidences of comparative myology, and, whenever possible, on developmental data. The muscles of branchiomeric origin are described first, then the myotomic muscles of the head and trunk, and finally, the muscles of the appendages.

Except where there is statement to the contrary, the innervation of each muscle was determined in several specimens of both genera of pocket gophers, and in most specimens of the squirrels and the aplodontia also. Innervation is doubtless the safest criterion of the homology of muscles, but when several muscles are supplied by the same nerve it is of less value and there seem to be exceptional instances in which it is even misleading (cf. Cunningham, 1881, 1882, 1891; Edgeworth *et al.*, 1929). Appleton (1928) has done important service to morphologists by calling attention to the importance of the topographical relationships of nerves and muscles, but this also may be modified (Hill, 1934). It seems necessary to take careful consideration of these two criteria and of the evidence of insertion. Ontological data is rare and fragmentary, but it will be important in the future.

I have followed most comparative anatomists in distinguishing muscles of branchiomeric origin from those which, in the lower vertebrates at least, are developed from the myotomes. Edgeworth (1929) and several other authors feel that this is not significant and is misleading, but the evidence seems to be in favor of the more generally accepted view.

#### BRANCHIOMERIC MUSCULATURE

**Masticatory group**—(figs. 11 and 12). Supplied by masticatory nerve.

*M. masseter*.—Rather full descriptions of this muscle in the Geomyidae have been published (Merriam, 1895; Tullberg, 1899). The nomenclature is involved; several sets of names have been proposed by different authors, and those who use the same names frequently use them with different significations. In rodents the masseter muscle is divided into five parts; three are of primary importance, the other two are subdivisions of two of the primary elements.

*M. masseter superficialis*. Synonymy.—

*M. masseter*—laterale [Portion], part, Hoffmann and Weyenbergh, 1870.

*M. masseter*—äussere Schicht, part, Teutleben, 1873 (*vide* Tullberg, 1899).

*M. masseter*—superficial tendinous layer, H. Allen, 1880.

Muscle masséter, insertion d'origine 3°, Kunstler, 1887.

*M. masseter*—anterior superficial part, Parsons, 1894a, 1896.

The masseter—rostral or superficial part, Merriam, 1895.

Masseter lateralis, portio superficialis, Tullberg, 1899.

Masseter lateralis superficialis, Miller and Gidley, 1918.

Masseter lateralis anterior, Hinton, 1926.

Masseter superficialis, Howell, 1926, 1932.

Masséter externe, part, Forster, 1929.

Origin, in pocket gophers, by ribbonlike tendon from ridge (or sunken line) ventral and slightly caudal to infraorbital foramen. Muscle fibers develop below eye on deep surface. Inserts on ventral margin and posterior border of mandible. In squirrels and *Aplodontia* some fibers pass around the ventral margin and insert on the medial surface of the mandible. In *Aplodontia* the superficial masseter muscle arises from the zygomatic process of the maxillary, but otherwise has the same relations as in other genera; the squirrels agree with the pocket gophers in the origin of this muscle.

*M. masseter lateralis profundus, pars anterior.* Synonymy.—

*M. masseter*—lateralis [Portion], part, Hoffmann u. Weyenbergh, 1870.

*M. masseter*—äussere Schicht, part, Teutleben, 1873 (*vide* Tullberg, 1899).

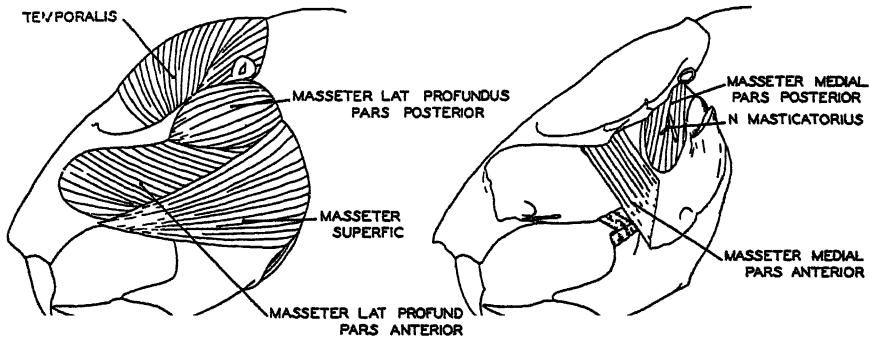


Fig. 11. Masticatory muscles (*Thomomys talpivorus*),  $\times 1$ .

*M. masseter*—second layer, part, H. Allen, 1880.

Muscle masséter, insertion d'origine 1°, Kunstler, 1887.

*M. masseter*—anterior deep part (sciuromorphic), part; —posterior superficial part (hystriocomorphine), part, Parsons, 1894a.

The main body of the masseter, part, Merriam, 1895.

*M. masseter*—posterior superficial part, part, Parsons, 1896.

*Masseter lateralis*, portio profunda, part, Tullberg, 1899.

*Masseter lateralis*, part, Miller and Gidley, 1918.

*Masseter lateralis posterior*, part, Hinton, 1926.

*Masseter major*, part, Howell, 1926.

*Masséter interne*, part, Forster, 1929.

*Masseter major*, all, Howell, 1932.

Arises from rostrum and adjacent zygomatic plate. Posterior fibers closely associated with pars posterior; they take origin from its aponeurosis and from the zygomatic arch. The muscle is largest in *Sciurus*, inserting on flattened area on lateral surface of mandible. In *Citellus* it is small; still smaller in *Aplodontia*. In these and in pocket gophers, insertion is tendinous, chiefly on masseteric ridge of mandible.

*M. masseter lateralis profundus, pars posterior.* Synonymy.—

*M. masseter*—lateralis [Portion], part, Hoffmann u. Weyenbergh, 1870.

*M. masseter*—äussere Schicht, part, Teutleben, 1873 (*vide* Tullberg, 1899).

*M. masseter*—second layer, part, H. Allen, 1880.

Muscle masséter, insertion d'origine 2°, Kunstler, 1887.

*M. masseter*—posterior superficial part (sciuromorphic); —posterior deep part (hystriocomorphine), part, Parsons, 1894a.

Zygomatic part of masseter, Merriam, 1895.

*M. masseter*—posterior superficial part, part, Parsons, 1896.

*Masseter lateralis*, portio profunda, part, Tullberg, 1899.

*Masseter lateralis*, part, Miller and Gidley, 1918.

*Masseter lateralis posterior*, part, Hinton, 1926.

*Masseter zygomaticus*, Howell, 1926.



Masséter externe, part, Forster, 1929.

Masseter posterior, Howell, 1932.

Origin from greater part of zygomatic arch. In pocket gophers smaller than anterior muscle and fibers run more caudad. Inserts on dorsal surface of angular process and alveolar tubercle. Small in *Sciurus*; larger in *Citellus*; the bulk of masseter in *Aplodontia*.

*M. masseter medialis, pars anterior.* Synonymy.—

M. masseter—mediale Portion, Hoffmann and Weyenbergh, 1870.

M. masseter—innere Schicht, part, Teutleben, 1873 (*vide* Tullberg, 1899).

M. masseter—third layer, H. Allen, 1880.

Muscle temporale (?), part, Kunstler, 1887.

M. masseter—anterior deep part (hystricomorphine), Parsons, 1894a.

The main body of the masseter, part, Merriam, 1895.

M. masseter—anterior deep part (all forms), Parsons, 1896.

Masseter medialis, portio anterior, Tullberg, 1899.

Masseter medialis, Miller and Gidley, 1918.

Masseter medialis anterior, Hinton, 1926.

Masseter major, part, Howell, 1926.

Masséter interne, Forster, 1929.

Masseter profundus, Howell, 1932.

Arises in pocket gophers from orbital surface of zygomatic plate and medial surface of zygoma. Fibers run almost vertically. Inserts by tendinous and fleshy fibers on anterior margin of coronoid process, its lateral surface, and on body of mandible. Similar in other rodents, except that in squirrels the part from the zygomatic plate is small. This part is large in *Aplodontia* where, contrary to the findings of Miller and Gidley (1918), no fibers passed through the infraorbital foramen in the specimens dissected by me (cf. Tullberg, 1896). Indeed, in *Aplodontia*, from the vertical direction of the muscle fibers, it would seem impossible for any of them to pass through the horizontal foramen.

*M. masseter medialis, pars posterior.*—This muscle has been overlooked by several investigators. Synonymy.—

M. masseter—innere Schicht, part, Teutleben, 1873 (*vide* Tullberg, 1899).

Suprazygomatic part of temporal, H. Allen, 1880.

M. masseter—posterior deep part, Parsons, 1894a, 1896.

Masseter medialis, portio posterior, Tullberg, 1899.

Masseter medialis posterior, Hinton, 1926.

Special slip of temporal, Howell, 1932.

Arises from medial side of posterolateral angle of zygoma. Fibers run cranioventrad; insert on ramus of mandible, below and in front of mandibular notch.

*M. temporalis.*—Large and important in pocket gophers. Superficial fibers partly separable from deeper ones. Former arise from dense superficial aponeurosis; insert on tip of coronoid process. Deeper fibers arise from superior nuchal line, sagittal or temporal ridge, and greater part of temporal fossa; insert on medial surface of coronoid process and depression between this and last two molar teeth. Anterior fibers take origin from temporal tuberosity ("postorbital" process, Merriam, 1895). Only minor differences were noted in the other forms, except in relative size.

*M. pterygoideus externus.*—Origin, lateral pterygoid plate and alisphenoid. Fibers run laterad, caudad, and slightly dorsad; insert on medial surface of neck of mandible.

**Internal pterygoid group.** Supplied by medial branch of mandibular nerve; this not followed, however, to tensor tympani.

*M. pterygoideus internus.*—In pocket gophers the pterygoid fossa from which this muscle takes origin is continuous with the sphenopterygoid canal which extends into orbit, permitting origin from lateral and medial pterygoid plates, and from presphenoid. Insertion, partly fleshy, partly tendinous, on marginal ridge of angle and depression on medial side of mandible anterior to this. In the squirrels and *Aplodontia* the muscle is large, but is restricted in origin to the shallow pterygoid fossa.

*M. tensor veli palatini*.—Arises from surface of tympanic bulla near anteromedial angle; passes dorsomedial to internal pterygoid muscle; inserts on soft palate, its tendon running over ventral margin of medial pterygoid plate, cranial to hamulus.

*M. tensor tympani*.—Dissected in specimens of *Thomomys bulbivorus* only. Arises from inner surface of bulla; attaches to manubrium mallei, near anterior process.

**Mylohyoid group** (fig. 12). Supplied by mylohyoid branch of mandibular nerve.

*M. mylohyoideus*.—Origin, groove ventral to alveoli of cheek teeth on medial side of mandible. Runs obliquely caudad; inserts on body of hyoid and on median raphe. Only minor differences in squirrels and *Aplodontia*.

*M. transversus mandibularis*.—Especially well developed in pocket gophers, although characteristic of rodents. Doubtless derived from the mylohyoideus muscle; relationships

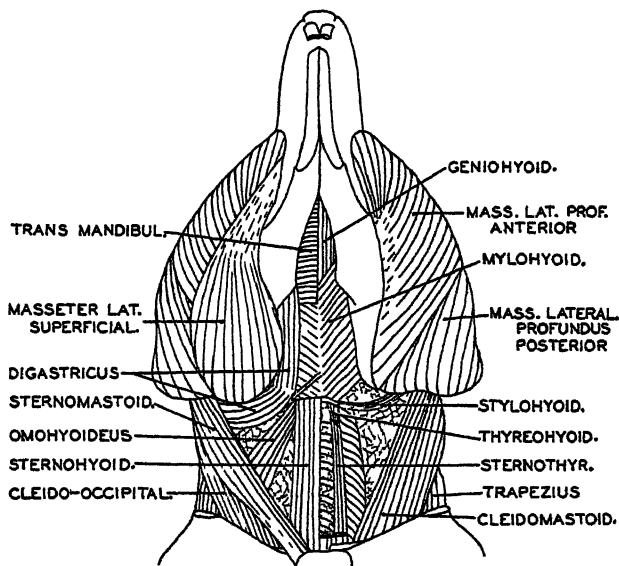


Fig. 12. Ventral muscles of head and neck (*Thomomys bulbivorus*),  $\times 1$ .

similar, supplied by same nerve. Runs transversely between halves of mandible, caudal to symphysis.

*M. digastricus*.—The mandibular belly of the digastric is peculiar to the mammals and appears to have been derived from the interramal muscle mass, some fibers of which came to take a longitudinal direction (cf. Edgeworth, 1914). In pocket gophers, posterior belly separated from anterior belly by slight constriction and some tendinous fibers, but no true tendon. Anterior part inserts on oblique ridge and fossa caudal to symphysis. Anterior belly separated from fellow. The squirrels and *Aplodontia* agree in exhibiting the "sciuromorphic" condition of the digastric (Parsons, 1894a): a tendon between anterior and posterior bellies, firmly attached to hyoid and to tendinous arch ventral to this; anterior bellies arise from this arch, in contact for most of lengths. In most muroid rodents (Parsons, 1896) the digastric is "sciuromorphic," but in some, *Neotoma* for example (Howell, 1926), the muscle is intermediate in character and the tendon is absent. The "sciuromorphic" type of digastric is probably the more primitive, being more like that in other orders of mammals, and the muscle in pocket gophers shows rudimentary features (the fascia which unites the two muscles and which attaches to the hyoid bone) which indicate that it passed through a stage comparable to that in the squirrels.

**Constrictor colli group** (figs. 13 and 14). Supplied by superficial branches of the facial nerve. Facial muscles in pocket gophers are of same general plan as in *Dipodomys* (Howell, 1932). Certain differences indicate less divergence from the primitive ground plan for

mammals (Huber, 1930, 1931); other differences are of a more advanced type. The muscles of the cheek pouches were described by McChesney (1878), but rather imperfectly. H. L. Osburn (1894) gives a better account and proposed names for several. Merriam (1895) and Holliger (1916) both describe these muscles, but add little to Osburn's account.

*M. sphincter colli primitivus*.—Two muscles appear to belong to this sheet which is partly deep, partly superficial to platysma. Howell (1932) found the two continuous in *Dipodomys*, but in pocket gophers there is differentiation in the direction of the fibers and they decussate on the surface of the pouch. Cervical part (levator of the pouch, Holliger) in *Thomomys* takes origin from middorsal line caudal to superior nuchal line for some 20 mm. Some fibers insert on skin of shoulder; majority attach to medial and lateral surfaces of pouch,

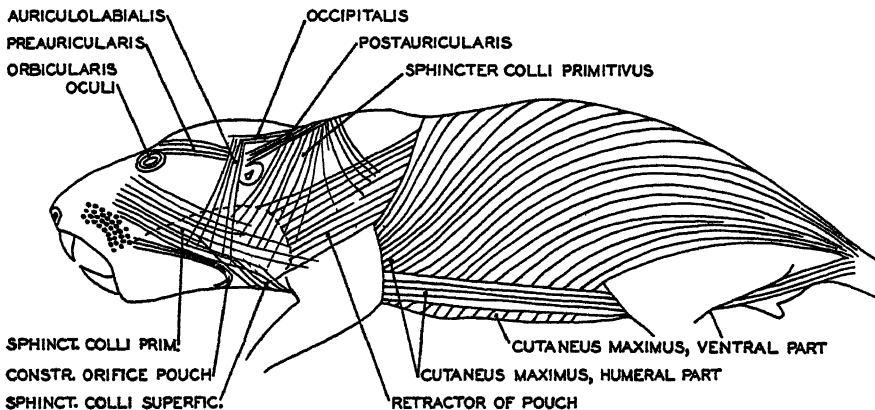


Fig. 13. Superficial facial muscles and *M. cutaneus maximus* (*Thomomys bulvivorus*),  $\times \frac{1}{2}$ .

enclosing platysma between two layers thus formed. Rostral part (protractor of the pouch, Osburn) arises from mystacial pad of connective tissue; runs caudad on lateral surface of pouch, decussating with cervical muscle. Some fibers extend beyond pouch; insert on skin of shoulder. In *Geomys*, levator of pouch less than half the width of that in *Thomomys*.

*M. sphincter colli superficialis*.—Thin sheet of muscle fibers arises from midventral line of throat; inserts on pouch and adjacent skin, superficial to other muscles. Howell (1932) did not find this muscle in *Dipodomys*.

*Retractor muscle of the pouch*.—Arises from superficial layer of lumbodorsal fascia and from spines of last two thoracic vertebrae, superficial to, and coextensive with, spinotrapezius. Runs parallel to latter muscle to spine of scapula; continues cranial to insert on caudal and dorsal margins of pouch. In *Thomomys* a small slip runs ventrad; attaches to superficial sphincter colli. Another slip (see fig. 14) arises from fascia of superficial sphincter; runs cranial to decussate with orbicularis oris. The two slips together seem to be homologous to a part of platysma which Howell (1932) figures in *Dipodomys* as "platysma lc." In *Geomys* these slips are absent; instead some fibers of the retractor muscle on medial side of pouch continue forward to lower lip and attach to orbicularis.

The anterior half of the retractor muscle of the pouch appears to represent the platysma, but the caudal half in *Thomomys*, *Geomys*, and *Dipodomys* apparently represents a part of the trapezius (Hill, 1935a) since it is supplied by the accessory nerve.

*M. postauricularis*.—Belongs to platysma layer (Huber, 1930, 1931); in pocket gophers divisible into deep layer from above epistropheus and more superficial layer arising more caudally. Deeper slip inserts on dorsocaudal surface of base of pinna; superficial muscle crosses obliquely and attaches to craniodorsal side of pinna, continuous with preauricularis.

*M. occipitalis*.—Related to the preceding and not separable from the superficial slip in *Geomys* and in some specimens of *Thomomys*. Inserts on skin between ears.

The intrinsic muscles of the ear were not dissected.

The rest of the facial muscles, according to Huber (1931), have been derived from *M. sphincter colli profundus*.

*M. interscutulatus* (not shown).—A few fibers in the superficial fascia, dorsal and medial to occipitalis, insert on the skin.

*M. preauricularis*.—Straplike, arising from frontal bone dorsal and medial to eye; inserts on anterior surface of ear and on superficial slip of postauricularis.

*M. auriculolabialis*.—Well developed in pocket gophers. Arises from fascia anterodorsal to ear; runs ventrad, spreading out on lateral surface of pouch.

*M. sternoauricularis*.—Origin, midventral line opposite first sternebra. Narrow and elongate. Runs deep to pouch; attaches to ventral surface of pinna. Some fibers insert on caudo-ventral angle of pouch (Holliger, 1916, calls this "ventral retractor of the pouch"). Contin-

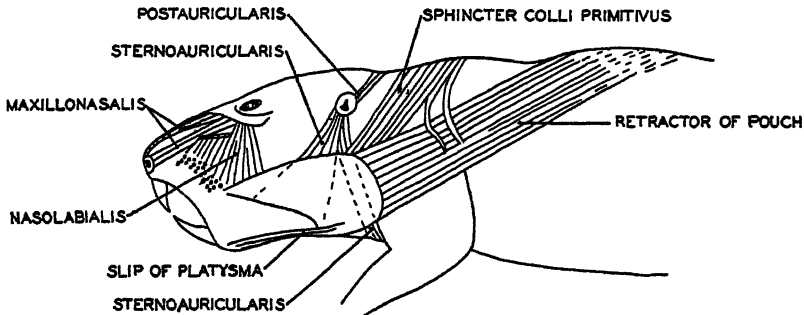


Fig. 14. Deep facial muscles (*Thomomys bulbivorus*),  $\times \frac{1}{2}$ .

uous with auricular insertion, a fan-shaped muscle runs ventrad inserting on anterior third of pouch, on its medial aspect. This muscle would seem to have been derived from the sternoauricularis.

*M. nasolabialis*.—Arises from rostrum and medial third of dorsal margin of zygomatic plate. Inserts on pouch and on mystacial pad of connective tissue.

*M. maxillonasalis* (not shown).—Apparently two muscles in pocket gophers: one, a slender slip from zygomatic plate near rostrum, ends in a tendon and inserts on dorsolateral side of rhinarium. Other, broader, lateral to preceding, runs along side of rostrum; attaches to side of rhinarium.

*M. maxillolabialis* (not shown).—Stout; arises from lateral groove of rostrum deep to nasolabialis. Inserts on lip near base of upper incisor.

*M. orbicularis oculi*.—Arises from hamulus of lacrimal and from fascia around eye.

*M. orbicularis oris* (not shown).—Origin from rostrum near incisor alveoli and from median line ventral to nostrils. Runs in lips; attaches to mandible; part forms a circle around base of lower incisor.

*M. buccinatorius* (not shown).—In pocket gophers modified to act as internal oral sphincter by insertion on large mystacial pad. When it contracts, pad pulled toward midline; closes mouth opening behind incisors. Origin from rostrum near base of incisors and from area anterior to origin of superficial masseter muscle. Additional attachment on mandible near base of premolar tooth.

*Sphincter muscle of the pouch*.—A thick band of fibers in the throat and cheek region on same plane as sternoauricularis closes the pouch opening. Inserts on pad of connective tissue containing the mystacial vibrissae.

The facial muscles were not preserved in the specimen of *Sciurus* nor in one of the specimens of *Citellus*. Consequently no detailed comparison of these muscles was attempted. It was observed that the cheek pouches in *Citellus* complicate the facial muscles in a different manner and to a lesser degree than in pocket gophers and their allies: the pouches have developed in the buccinator, deep to the platysma, inside the oral sphincter; deep layer of platysma attaches to caudal border; superficial layer lies lateral to sac (cf. Sleggs, 1926; Schreiber, 1929). The muscles of the cheek pouches in *Cricetus* (Parsons, 1896) are similar to those in *Citellus*.

**Hyoid constrictor group** (fig. 12). The deep muscles supplied by the facial nerve are considered by Edgeworth (1914) to have been derived from ventral constrictor of hyoid arch.

*M. digastricus*.—(Anterior belly described above with mylohyoid group.) Posterior belly arises from lateral half of jugular process. Near angle of jaw, a slight constriction; from medial surface a slender tendon runs forward to insert on median raphe of mylohyoid muscle. Fascia unites digastric at this point to its fellow and to hyoid.

*M. stylohyoideus*.—Slender, spindle shaped in pocket gophers. Origin by short tendon from anterior tubercle of jugular process. Runs on anteromedial surface of digastric; inserts on posterior horn (greater cornua) of hyoid. In squirrels and *Aplo dontia*, stylohyoid arises from stylohyal cartilage and inserts by a tendon. With the reduction of the anterior horn of the hyoid, the stylohyoid appears to have migrated to the jugular process.

*M. jugulohyoideus*.—With the loss of the stylohyal cartilage in pocket gophers and in muroid rodents, this muscle also disappears; but it is present in squirrels and in *Aplo dontia*. Arises from jugular process; inserts on stylohyal cartilage opposite origin of stylohyoid and styloglossal muscles. Not mentioned by Hoffmann and Weyenbergh (1870) nor by Parsons (1894a).

*M. stapedius*.—Not found in specimens of pocket gophers examined, but possibly overlooked.

**Glossopharyngeal group** (fig. 12). Supplied by glossopharyngeal nerve.

*M. stylopharyngeus*.—The only muscle of this group dissected. Slender in pocket gophers; arises from anterior tubercle of jugular process, with stylohyoid and styloglossal muscles. Separated from former by external carotid artery, from latter by glossopharyngeal nerve. Inserts on craniolateral border of thyroid cartilage and on lateral wall of pharynx.

The pharyngeal and laryngeal muscles supplied by the vagoaccessory and vagus nerves were not investigated.

**Trapezius group** (figs. 12 and 15). There is still some uncertainty concerning the origin of this group, chiefly because of the dual innervation of these muscles: from the accessory and from the second and third spinal cervical nerves (cf. Nishi, 1922). It seems probable that these muscles belong to the branchiomeric series, and that the cervical innervation is secondary or indicates a fusion of some myotomic elements with the visceral elements. Muscles of similar relations in the anamniotes are supplied by the vagus nerve, and the ramus externus of the accessory nerve, the fibers of which supply these muscles in man, arises from the special splanchnic efferent column of the spinal medulla in series with the nucleus ambiguus (Paterson, in Cunningham, 1927; Herrick, 1932). Ontogenetically, the group arises from the mesenchyme of the branchial arches (Edgeworth, 1911; Lewis, 1910).

The trapezius has divided differently in different mammals so that exact homologies are probably lacking, but the sternocleidomastoid muscles in rodents are more definitely comparable to those in other mammals.

Three muscles together represent the human sternocleidomastoid.

*M. sternomastoideus*.—Most robust of the three. Arises by tendinous and fleshy fibers from craniolateral surface of manubrium sterni; inserts on ventrolateral margin of mastoid process of squamosal. In *Geomys*, petromastoid element in mastoid process is larger; some fibers attach to it also; sternomastoid more flattened in this genus than in *Thomomys*.

*M. cleidomastoideus*.—Deep and lateral to preceding, fan-shaped. Arises from clavicle for most of medial three-fifths; converges; inserts in continuity with sternomastoid on tip of mastoid process.

*M. cleido-occipitalis*.—Although continuous with trapezius in origin and insertion, separated from that muscle by great auricular nerve and its branches. Arises from third lateral quarter of clavicle, more medial fibers lying deep to cleidomastoid; runs obliquely; inserts on superior nuchal line, between trapezius and sternomastoid.

In *Dipodomys* the cleido-occipitalis is present, but small. It is well developed in *Neotoma*, where Howell (1926) identified it with the clavicular part of trapezius. Wood (1870), who first described and named this muscle, found it in the Norway rat and in a number of other

mammals. In the squirrels and *Aplodontia*, except for a more intimate association between sternomastoid and cleidomastoid, these muscles are not distinctive.

*M. trapezius*.—Separable in pocket gophers into three parts, connected by a thick sheet of fascia indicative of their original continuity.

*M. acromiotrapezius*.—Probably corresponds to clavicular and acromial parts of trapezius of other mammals. Origin, medial three-fourths of superior nuchal line and middorsal line, cranial to spine of fourth thoracic vertebra. Caudal three-quarters of latter part of origin, aponeurotic. Inserts on lateral fifth of clavicle, on acromion, and on spine of scapula.

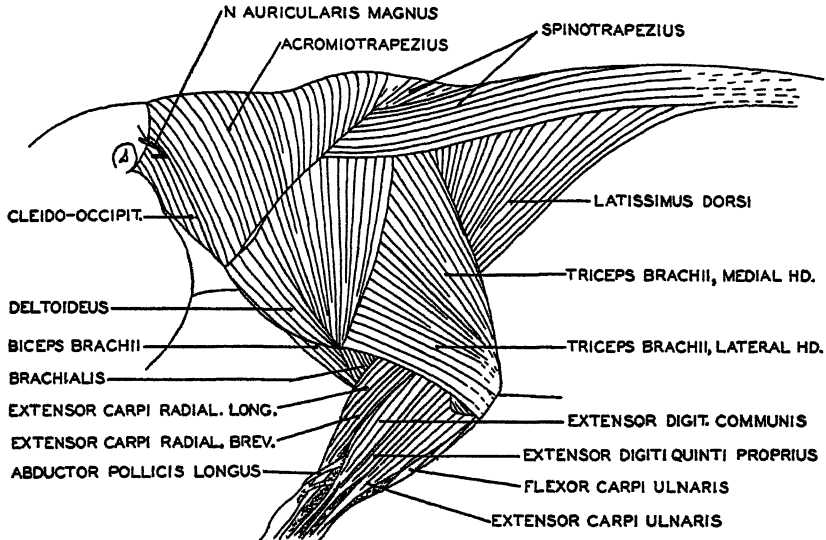


Fig. 15. Superficial lateral muscles of shoulder and forelimb (*Thomomys talpivorus*),  $\times 1$ .

*M. spinotrapezius*.—Divided into two unequal muscles. Smaller arises from spines of sixth and seventh thoracic vertebrae; converges to tendon; inserts on crest of scapular spine. Larger part straplike; runs from lumbodorsal fascia and spines of last two thoracic vertebrae and first two lumbar to spine of scapula and crest.

In *Dipodomys* the clavicular insertion is vestigial, and the spinotrapezius is undivided. In squirrels and in *Aplodontia* the trapezius is single as in primates. This I conclude to have been the primitive mammalian condition, retained by many forms.

### MYOTOMIC MUSCULATURE

**Ocular muscles.** The muscles of the eyeball do not exhibit noteworthy peculiarities. The eye is reduced in size in pocket gophers, but the muscles controlling its movement are well developed. The four rectus muscles are long, straplike; insert on eyeball opposite equator of lens. Inferior oblique arises from zygomatic plate; runs horizontally; inserts superficial and lateral to inferior rectus. Superior oblique arises near superior rectus; lies on medial wall of orbit parallel with frontal nerve; ends in a slender tendon, which passes over fibrous trochlea; inserts on eyeball external to superior rectus and between this and lateral rectus. Retractor oculi a continuous band, inserting on eyeball deep to rectus muscles. Levator palpebrae superioris, straplike; lies superficial to superior rectus from which it was probably derived.

**Lingual muscles** (fig. 12). Supplied by the hypoglossal nerve.

*M. genioglossus*.—Origin from mandible, deep to origin of geniohyoid. Spreads out fanwise; inserts on tongue; a few medial fibers, in pocket gophers and *Aplodontia*, attach to hyoid. In *Citellus* the muscle is attached to the hyoid by fascia.

*M. hyoglossus*.—Arises from lateral moiety of hyoid; runs craniolaterad; inserts on tongue. In *Citellus* and *Aplodontia* this muscle runs in a more lateral direction than in pocket gophers, and is wider.

*M. styloglossus*.—Slender in pocket gophers; runs ventrocraniad from anterior tubercle of jugular process to tongue. In squirrels and in *Aplodontia* it is stouter; arises from stylohyal cartilage, in continuity with insertion of jugulohyoid.

The intrinsic muscles of the tongue do not show any difference from these muscles in man, except that the vertical muscle is disproportionately large.

### *Muscles of the body*

#### DORSAL DIVISION

The epaxial muscles are supplied by branches of the dorsal rami of spinal nerves. The particular nerves supplying each muscle were not determined, however.

##### Superficial spino-occipital group.

*M. splenius*.—In pocket gophers, as in other rodents (except for a few hystricomorph types, Parsons, 1894a, 1896), a vertebral insertion is absent. Arises from nuchal ligament for most of its length; inserts on superior nuchal line for almost its entire extent.

##### Sacrospinalis group.

*M. sacrospinalis*.—Origin, crest of ilium, lumbar and sacral vertebrae, and ribs. Before divisible into component parts, fibers insert on transverse processes of lumbar vertebrae. Since these processes are serially homologous to ribs, the slips probably should be considered as representing part of the iliocostalis.

*M. iliocostalis*.—Lumbar part inserts on last six ribs. Dorsal part attaches to third to sixth ribs inclusive; cervical part inserts on first rib and last three cervical vertebrae. Each slip of dorsal and cervical parts passes over three ribs before inserting on fourth. In the squirrels and *Aplodontia* it inserts on all ribs.

*M. longissimus*.—Inserts on caudal ten ribs and on accessory processes of thoracic and lumbar vertebrae. In cranial part of thorax attaches to undivided transverse processes. Bundles arise from mamillary processes; pass over two vertebrae to insert on third. More segments are skipped by the bundles which insert on ribs. Longissimus cervicis is continuous with the dorsal muscle; inserts, in pocket gophers, on transverse processes of all cervical vertebrae. Insertion restricted to last three cervical vertebrae in squirrels, and to fourth and fifth in *Aplodontia*. Longissimus capitis absent in pocket gophers. In squirrels and in *Aplodontia* it is present; arises from transverse processes of cervical vertebrae; inserts on superior nuchal line near mastoid process.

*M. extensor caudae lateralis*.—In pocket gophers (and in *Aplodontia*) with the reduction of the tail, this muscle is largely postsacral. Origin from transverse processes of last two sacral and first few caudal vertebrae. Inserts on articular processes of caudal vertebrae. In mammals with well-developed tails, such as *Neotoma* (Howell, 1926), *Dipodomys*, and squirrels, a noticeable presacral part arises from the accessory processes of most lumbar vertebrae and the last two thoracics.

*M. spinalis dorsii*.—Absent in pocket gophers, but in squirrels and *Aplodontia*, fibers united with semispinalis exhibit the general relations of this muscle.

**Semispinalis group.** Includes muscles, the fibers of which arise from transverse processes and insert on spines or lamellae of vertebrae.

*M. semispinalis capitis*.—In pocket gophers large, indivisible. Origin, transverse processes of first nine thoracic and last six cervical vertebrae. Inserts on medial two-fifths of superior nuchal line. Medial part, *M. biventer cervicis*, easily separable in squirrels and *Aplodontia*. Whether separable or not, this part, in all, inserts by fleshy fibers, whereas the lateral part inserts by an aponeurosis (cf. Parsons, 1894a). In *Aplodontia* the lateral muscle exhibits a single tendinous inscription, whereas biventer cervicis exhibits several; in the other genera these inscriptions are absent.

*M. semispinalis*.—Apparently includes multifidus and rotatores. Arises from mamillary processes of lumbar and last few thoracic vertebrae and from transverse processes of other thoracics. In the lumbar region most fibers pass over a single segment to insert on the spine of the second vertebra craniad, but the more cranial fibers may pass over as many as seven segments. In the neck the muscle attaches to the large spine of the axis; and some of the deeper fibers attach to the spines of the last five cervical vertebrae.

*M. extensor caudae medialis*.—Continuous with preceding; arises from spines of sacral and of first several caudal vertebrae. Inserts on transverse processes of caudal vertebrae, usually passing over two vertebrae to do so.

**Suboccipital group.** *Mm. recti capites posterior* and *obliqui capites* have much the same relationships as they do in man; no important differences were found in squirrels or *Aplodontia*.

## VENTRAL DIVISION

The muscles of the ventral division include all remaining skeletal muscles of both body and appendages. Branches of the ventral rami of spinal nerves supply these muscles. It is not possible to homologize satisfactorily muscles of the appendages with those of the body wall, so it is thought advisable to treat them separately.

**Cervical prevertebral group.** Supplied by branches arising from the ventral rami as these emerge from the intervertebral foramina.

*M. rectus capitis anterior*.—Arises from ventral margin of transverse process and ventral arch of atlas. Inserts by fleshy fibers into fossa in basal part of occipital.

*M. longus capitis*.—Arises chiefly from carotid tubercle of sixth cervical vertebra. Fibers also arise from areas similar in position on fourth and fifth vertebrae. Inserts on tuberosity near occipitospheonoid suture. Twigs from ventral rami of second to sixth cervical nerves innervate this muscle.

*M. longus colli*.—Two parts. Cephalic part arises from ventral surface of sixth cervical vertebra and from ventral parts of third to sixth cervical transverse processes; inserts on ventral tubercle of atlas; additional attachments on bodies of second to sixth cervical vertebrae. Caudal part arises from heads of first two ribs and from lateroventral surfaces of first three thoracic and last cervical vertebrae; inserts on ventral tubercle of transverse process of sixth cervical. Twigs from ventral rami of cervical nerves supply this muscle.

**Lumbar prevertebral group** (fig. 21).

*M. quadratus lumborum*.—Lies between psoas minor and sacrospinalis. Origin by tendons from transverse processes of first sacral and last five lumbar vertebrae. Insertion by tendons on caudolateral angle of bodies of last two thoracic vertebrae, by fleshy fibers on lateral surfaces of first three lumbar vertebrae, on their transverse processes, and on the last rib or two. In *Aplodontia* and in squirrels it inserts on the last three or four thoracic vertebrae and ribs; otherwise similar.

*M. psoas minor*.—Derived, according to Gregory and Camp (1918), from quadratus lumborum; from its relationships this seems likely. Bardeen (1906), however, states that in man it appears to develop from the iliopsoal anlage, but he was not positive. Origin, iliopectineal eminence; insertion, bodies of first five lumbar vertebrae, its ribbon-like tendon passing over ventromedial surface of psoas major. Supplied by branches of lumbar nerves.

**Caudal flexor group** (fig. 21).

*M. flexor caudae lateralis*.—Arises from pelvic surface of ilium, cranial to origin of iliocecygeus. Two parts, one more cranial in position than the other. In squirrels it is larger than the medial muscle; it arises from the last lumbar and from sacral and caudal vertebrae. In *Aplodontia* it is small, hardly separable from the medial muscle; its origin is restricted to the sacrum.

*M. flexor caudae medialis*.—In three parts. Most cranial part is the most lateral; arises from bodies and transverse processes of second and third sacral vertebrae. Intermediate part takes origin from bodies of second to fifth sacra. Small caudal part arises from first two caudal vertebrae. It is indivisible in *Citellus*, but in *Sciurus* there are two parts. In *Aplodontia* there are three parts as in pocket gophers. This muscle and the preceding one



insert on chevron bones of tail and on ventral surfaces of caudal vertebrae. Supplied by branches of sacral and caudal nerves.

**Medial ventral cervical group** (fig. 12). The muscles of this group develop ontogenetically from a single rudiment (Edgeworth, 1916). The geniohyoid is supplied by the hypoglossal nerve; the infrahyoid muscles by a special nerve arising from the loop between the first and second cervical nerves, completely independent of the hypoglossal.

*M. geniohyoideus*.—Large in pocket gophers; probably important in mastication, assisting the digastric to open the mouth and retract the lower jaw. Attached, by fleshy fibers, to a fossa behind symphysis of mandible. In contact with its fellow; near attachment to hyoid the two become inseparable (cf. Parsons, 1894a, 1896). In squirrels and in *Aplodontia* the geniohyoid is smaller; it inserts by a slender tendon on the mandible.

*M. sternohyoideus*.—Origin, deep surface of sternum near joint between manubrium and first sternebra, and deep surface of costal cartilage of second rib; insertion, hyoid bone. Sternohyoid muscles in contact, but distinct.

*M. sternothyreoideus*.—Slender; arises from fascia of sternohyoid on its deep surface; inserts on oblique line of thyroid cartilage. It is similar in *Citellus* and *Aplodontia*, but in *Sciurus* it is larger, more distinct from the sternohyoid.

*M. thyreochoideus*.—Short and small. Arises in continuity with insertion of sternothyroid from side of thyroid cartilage; inserts on dorsocaudal surface of hyoid.

*M. omohyoideus*.—Larger in pocket gophers and in *Aplodontia* than usual. Origin, cephalic border of scapula; insertion, hyoid, deep and lateral to attachment of sternohyoid. There is an inscription in *Aplodontia*, but in none of the others (cf. Parsons, 1894a).

**Medial thoraco-abdominal group.**

*M. rectus abdominus*.—Attaches, in pocket gophers, to hip bone, to first rib, and to manubrium sterni. Wide in abdominal region. Several tendinous inscriptions in cranial part, but poorly marked compared to those in man. Caudal part divided; lateral fibers unit with external oblique and arise with it from ventrocranial border and ventral tuberosity of hip bone. Medial part in *Geomys* becomes tough aponeurosis, forming floor of pelvis in both sexes. In *Thomomys*, fibers decussate with those of the opposite side; attach to symphysis in male specimens, to symphyseal ligament in females, and in both sexes, to adjacent hip bone. Chapman (1919) found variation of a minor nature in different species of *Thomomys*. In squirrels and in *Aplodontia* the rectus is simple and nearly straight. In the former rodents, it arises from the symphysis without decussation; in *Aplodontia*, however, it decussates.

**Lateral cervical group.** Supplied by dorsal branches of ventral rami of cervical nerves; scalenus is also innervated by the first two or three intercostal nerves.

*M. rectus capitis lateralis*.—Arises from transverse process of atlas; inserts on medial ridge and medial half of jugular process.

*M. scalenus*.—The scalenus muscles in rodents cannot be homologized with those in man with any degree of assurance, since the part ventral to the brachial plexus is absent, except in *Gerbillus* and in a few hystricomorph types (Parsons, 1894a, 1896). Two partly distinct muscles in pocket gophers. The more dorsal arises by a strong tendon from transverse process of atlas; inserts on third, fourth, and fifth ribs (third and fourth ribs only in *Geomys*). Fibers attaching to last one or two ribs, pass between slips of serratus anterior from third and fourth ribs. Ventral muscle arises from tendon of origin of dorsal muscle and from ventral parts of transverse processes of last six cervical vertebrae. Inserts on dorsal parts of last six cervical vertebrae and on cranial surface of first rib. The scalenus complex agrees with this description in squirrels and in *Aplodontia*, except that in the latter, the dorsal muscle attaches to the first and second ribs also. Judging from the cervical insertion, the ventral muscle contains bundles which represent the lateral intertransversarii. In the neck region the scalene muscles are separated from the epaxial muscles by *M. levator scapulae*, so it seems improbable that there are any epaxial elements present in the scalenus complex of rodents, whether or not such may be found in other mammals (cf. Howell, 1932).

**Lateral thoracoabdominal group.** These muscles are supplied by the intercostal and first lumbar nerves and the inguinal nerve. Malsley (1915) presents evidence that the views of Gegenbaur regarding the homologies of the muscles of this group are to be accepted. That is,

the external oblique is homologous to the external intercostal muscles; the internal oblique to the internal intercostals; the transversalis abdominis to the transversalis thoracis.

The intercostal muscles agree with the description of these muscles in other mammals, and the oblique and transverse muscles of the abdomen exhibit only minor differences. The inguinal ligament is well developed in pocket gophers, but it is hardly differentiated in the other genera examined.

*M. serratus posterior superior*.—Arises from middorsal line between shoulder blades, over first six thoracic vertebrae. Cranial third is aponeurotic for short distance from origin. Runs caudoventrad to insert on cranial side of fifth to tenth ribs inclusive, near middle of bodies (in some specimens on fourth rib also). Fascia unites to serratus posterior inferior.

*M. serratus posterior inferior*.—Arises by long aponeurosis from middorsal line and from spines of last four thoracic and first two lumbar vertebrae. Inserts by fleshy slips on caudal surface of last three or four ribs. Caudal margin continuous with origin of internal oblique and inseparable from it. Runs ventrocraniad, obliquity increasing toward caudal end. In *Aplodontia* the serratus posterior muscles are continuous, differentiated only by the direction of their fibers.

*M. sternocostalis*.—Arises from midventral line; passes ventrally over rectus abdominis; inserts on first rib. Supplied by second intercostal nerve; appears to be detached part of external oblique, as Keith concluded (1894b). Parsons (1896) states that this muscle is usually absent in rodents, but it is present in pocket gophers, squirrels, and *Aplodontia*, as well as in *Dipodomys* and *Allactaga* (Howell, 1932).

*Mm. subcostales*.—Well marked; not restricted to more caudal ribs in pocket gophers as they are in man, but arise from all except first two ribs, from their pleural surfaces and from first two lumbar transverse processes. Each muscle passes over one rib to insert on caudal surface of second rib craniad, on angle and dorsal third of body.

*Mm. levatores costarum*.—Small slips, arising by tendons from accessory processes, or from homologous parts of transverse processes. Run caudoventrad; insert on ribs near angles.

*M. transversalis thoracis*.—Arises from internal surface of xiphisternum and sternbrae; inserts on costal cartilages of second to tenth ribs. Caudal part the more extensive.

**Diaphragma.** Supplied by the phrenic nerve. Crura arise by tendons and fleshy fibers from bodies of second to fifth lumbar vertebrae. Other fibers arise from transverse fascia of abdomen, from margins of costal cartilages of last several ribs, and from xiphisternum. Central tendon irregularly circular; contains openings through which pass inferior vena cava and esophagus. Opening for aorta situated between crura, approximately opposite first lumbar vertebra.

**Perineal group.** Supplied by branches from the sacral plexus. Includes the perineal muscles and certain muscles of the tail. This group dissected in *Thomomys* only.

*M. iliococcygeus*.—Stout, in pocket gophers and squirrels, but apparently absent in *Aplodontia*. Origin, pelvic surface of hip bone, dorsal to iliopectineal eminence. Insertions, ventral surfaces of caudal vertebrae by a number of slender tendons.

*M. pubococcygeus*.—Fan-shaped. Origin, ventral margin of obturator foramen and hip bone caudal to this. Insertion, lateroventral side of caudal vertebrae, tendons of other flexors of tail, and transverse processes of first several caudal vertebrae.

*M. coccygeus*.—Represented in *Thomomys* by sacrospinous ligament, containing few muscle fibers. Attaches to spine of ischium and transverse processes of last one or two sacral vertebrae. In *Geomys* replaced by bony tissue, forming a bridge between ischium and sacrum, whereas in *Dipodomys* the structure is muscular (Howell, 1932). The latter condition is found in squirrels. It is large in *Aplodontia*; the cranial third largely ligamentous, the rest fleshy.

*M. sphincter ani*.—The external and internal sphincter muscles of the rectum are inseparable, forming a wide muscular ring around the anal orifice and rectum.

*M. rectocavernosus*.—Present in both male and female, but better developed in former. Appears to be part of sphincter cloacae, since continuous with sphincter ani dorsal to rectum. Inserts on crura of penis, or of clitoris.

*M. bulbocavernosus*.—Present in both sexes; weak in females, in which it surrounds vaginal orifice, inserting on crura of clitoris. Larger in males, surrounding corpus cavernosus urethrae and its bulbous expansion.

*M. ischiocavernosus*.—Small in females, but distinct; larger in males. Arises from caudomedial surface of ventral ischial tuberosity and from hip bone ventral to this. Nearly surrounds crus penis, or crus clitoridis, inserting on these structures.

*M. sphincter urethrae membranaceae*.—Found only in males. Surrounds urethra from entrance of ejaculatory ducts to entrance of bulbo-urethral ducts.

There is no *M. retractor penis*.

### Appendicular Musculature

The limb muscles are divided into extensor and flexor systems, supplied by dorsal and ventral branches, respectively, of the brachial and lumbosacral plexus. These systems are further subdivided into groups of similar morphological relationships. The phylogeny of the muscles of the proximal segments of the limbs has been discussed by Gregory and Camp (1918); that of the flexor system of the distal segments by McMurry (1902*a* and *b*, 1903, 1904, 1907).

#### MUSCLES OF THE PECTORAL GIRDLE AND LIMB

##### EXTENSOR SYSTEM

**Costo-spino-scapular group** (fig. 16). In rodents, as in many other mammals (Leche, 1900), levator scapulae and serratus anterior are parts of a single muscle sheet. Rhomboideus, occipitoscapularis, and omocervicalis are closely related to one another, and only a little less closely to the others, as indicated by their insertion, phylogenetic history, ontogeny (Lewis, 1910), and innervation.

*M. levator scapulae et M. serratus anterior*.—A single sheet, except for the slip from the atlas, arising from transverse processes of atlas and last four cervical vertebrae and from ventral parts of first eight or nine ribs. Converges to insert on entire length of vertebral border of scapula and on its adjacent costal surface. Thoracic part arises by slips; cervical part undivided. Supplied, caudal to sixth cervical vertebra by long thoracic nerve, more cranially by three dorsal scapular nerves.

*M. rhomboideus*.—Single, in pocket gophers, arising from middorsal line, dorsal to last six cervical vertebrae and first four thoracics. In *Geomys* it is continuous with occipitoscapularis. Inserts on vertebral border of scapula, the fibers running obliquely laterocaudad.

*M. occipitoscapularis*.—Frequently called "rhomboideus capitis," "levator scapulae dorsalis," etc. (cf. Leche, 1900). Large; origin, lateral half of superior nuchal line, deep to trapezius. Insertion in continuity with rhomboideus, on lateral margin of vertebral border of scapula, cranial to spine; also attaches to spine, ventrad nearly as far as acromion. It is smaller in *Sciurus*, restricted to the vertebral border of the scapula. In *Citellus*, part inserts on the spine. In *Apodonta*, it is large; its insertion much as in pocket gophers.

*M. omocervicalis*.—This muscle has different attachments in different mammals, and consequently has received a number of names: "levator scapulae ventralis," "levator clavicularis," "atlantoscapularis," and "basioclavicularis." The primitive origin seems to be the transverse process of the atlas; the primitive insertion is the acromion. Both attachments are retained by numerous unrelated animals, but either one or the other may be modified. Usually, however, if one attachment migrates, the other remains. The primitive origin and insertion are both present in *Heteromys* (Parsons, 1896) and in *Neotoma* (Howell, 1926). In *Dipodomys* (Howell, 1932) insertion is partly on the clavicle, partly on the tip of the acromion. In the pocket gophers insertion is restricted to the lateral quarter of the clavicle. In squirrels and in *Apodonta* the acromial insertion is retained, but the origin has migrated to the ventral arch of the atlas in *Sciurus* and *Apodonta*, to the basioccipital in *Citellus*.

Branch from second cervical nerve supplies omocervicalis in pocket gophers.

**Latissimus-subscapular group** (figs. 15, 16, and 17). Judging from similarity of innervation, and from insertions, latissimus dorsi, teres major, and subscapularis appear to be related. The relationship of the first two of these is somewhat closer than that between either of these and the subscapularis. The teres major and the latissimus develop ontogenetically from a single muscle mass in man (Lewis, 1910). The scapular slip of the latissimus in man and some other mammals (Leche, 1900) indicates how the teres major may have become differentiated. Supplied by subscapular nerves, most caudal of which, usually called thoracodorsal, innervates latissimus dorsi.

*M. latissimus dorsi*.—Origin, spines of last four or five thoracic and first lumbar vertebrae, and lumbodorsal fascia. Partly covered superficially by trapezius. Converges to a stout ribbonlike tendon; inserts on medial ridge of humerus with teres major, and medial to it. In squirrels and in *Aplodontia*, latissimus dorsi retains its primitive origin from the more

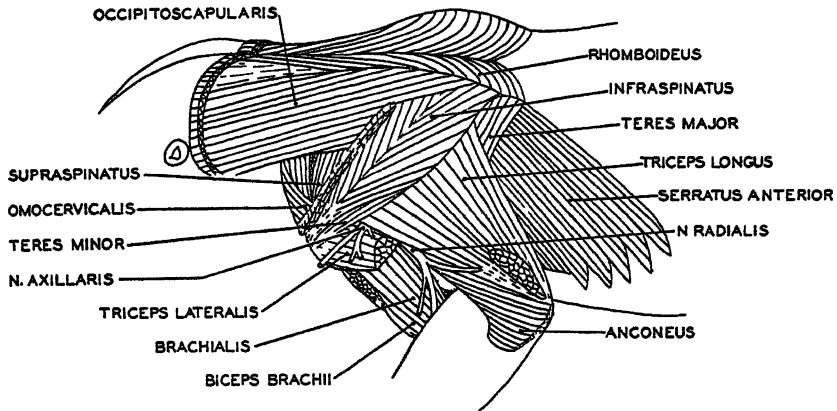


Fig. 16. Deep lateral muscles of shoulder and upper arm (*Thomomys bulbivorus*),  $\times 1$ .

caudal ribs (cf. Leche, 1900). In *Aplodontia*, teres major partly unites with latissimus, and part of latissimus forms an "achselbogen," such as described by Heidrich (1906) in the cat.

*M. teres major* (fig. 17).—Straplike, arising from teres major fossa on caudal angle of scapula and from axillary ridge. Inserts with latissimus dorsi by a flat tendon on medial ridge of humerus. In the squirrels conditions are similar, but in *Aplodontia*, the insertion is fleshy, partly on the tendon of latissimus dorsi, partly on the medial ridge in continuity with the insertion of *M. subscapularis*. A branch of the third subscapular nerve supplies teres major.

*M. subscapularis* (fig. 17).—Subdivided into four bipennate parts. The tendons that are formed converge to insert on lesser tubercle of humerus. Axillary nerve and vessels and short part of coracobrachialis, separate subscapularis from the rest of the group. In squirrels and in *Aplodontia*, the muscle is less subdivided. Supplied by three subscapular nerves.

**Deltoid group.** Supplied by the axillary nerve.

*M. deltoideus* (fig. 15). Hardly more divided in pocket gophers and in *Aplodontia* than in man. In squirrels, however, it is separable into acromioclavicular and spinal parts. Arises from lateral three-quarters of clavicle, from acromion, from spine of scapula, and from fascia of infraspinatus. The part which arises from the spine is smaller in *Geomys* than in *Thomomys*.

*M. teres minor* (fig. 16).—Small and bipennate. Arises from distal half of axillary ridge and from adjacent area of infraspinous fossa. Inserts on greater tubercle, caudal to infraspinatus.

**Suprascapular group**<sup>1</sup> (fig. 16). Supplied by the suprascapular nerve.

*M. infraspinatus*.—Bipennate; arises from infraspinous fossa, spine, and axillary ridge; inserts by tendons on dorsocaudal side of greater tubercle.

<sup>1</sup> Recently Howell (1936: Anat. Record, 66:307) considers this group to belong with the flexor system, closely related to pectoralis major.

*M. supraspinatus*.—Bipennate, broader and stouter than *infraspinatus*. Origin, supraspinous fossa, cranial surface of spine, and intermuscular septum between supra- and *infraspinatus*. Inserts by tendon on cranial part of greater tubercle.

**Triceps group** (figs. 15, 16, and 17). The parts of *M. triceps* are almost as distinct from one another as they are from the other two members of the group, *M. anconeus* and *M. dorsoepitrochlearis*. The radial nerve supplies these muscles.

*M. triceps brachii*.—Three heads more distinct in rodents than in man. *Caput longum* largest; in *Thomomys*, incompletely separable into superficial and deep parts. The former, triangular and flattened, arises from distal three-quarters of axillary border of scapula.

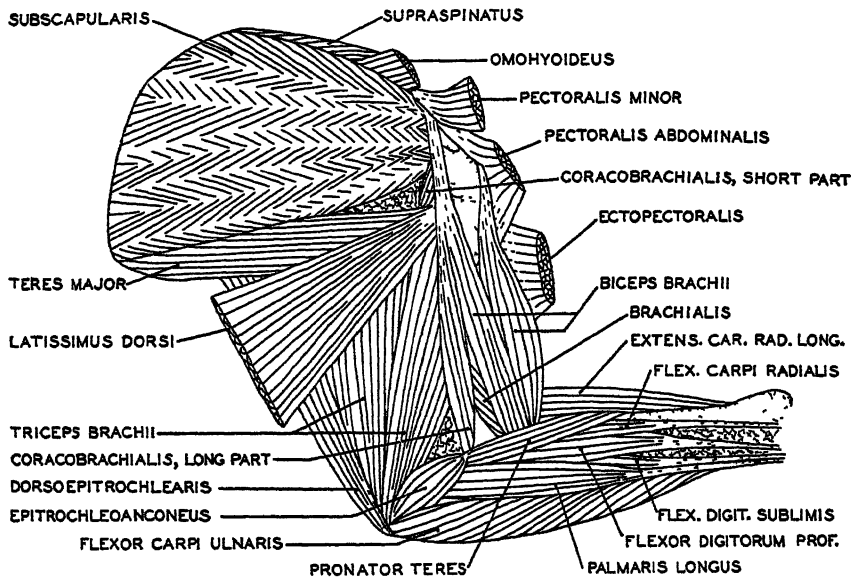


Fig. 17. Medial muscles of shoulder and forelimb (*Thomomys bulbivorus*),  $\times 1\frac{1}{2}$ .

Deeper part more spindle-shaped; origin from infraglenoid tuberosity by a short, stout tendon. *Caput laterale* arises from greater tubercle and lateral surface of humerus. *Caput mediale* arises from caudomedial surface of humerus, between insertions of teres major and coracobrachialis, and between origins of brachialis and anconeus. Inserts on medial and dorsocranial surfaces of olecranon. In *Geomys* the long head is single, relatively larger than in *Thomomys*. In both genera of squirrels and in *Aplodontia* the muscle is more restricted in origin, more compact.

*M. anconeus*.—Moderate in size, triangular. Arises from caudal surface of lateral epicondyle and epicondylar ridge; inserts on lateral surface of olecranon. In pocket gophers it is separable with difficulty from the medial head of triceps; even less differentiated in squirrels and in *Aplodontia*.

*M. dorsoepitrochlearis*.—Apparently derived from long head of triceps; inserts with that muscle and is supplied by a branch of its nerve. Origin, in *Thomomys*, lateral surfaces of latissimus dorsi and teres major; in *Geomys* and in squirrels from fascia of teres major and from proximal fourth of axillary ridge of scapula in continuity with long head of triceps. In *Aplodontia* it arises from the surface fascia of latissimus dorsi.

**Extensor group of the forearm** (figs. 15 and 17). *M. brachioradialis*, when present, and *M. extensor carpi radialis longus* are supplied by the radial nerve before it divides; the other muscles are supplied by the deep ramus and the dorsal interosseous nerve.

*M. brachioradialis*.—Absent in pocket gophers and kangaroo rats, as in muroid rodents (Parsons, 1896). Also absent in *Aplodontia* and, according to Parsons (1894a), in *Castor*. In squirrels, however, it is large; arises from cranial surface of lateral epicondylar ridge; inserts on distal end of radius at base of styloid process.

*M. extensor carpi radialis longus*.—Slender, spindle-shaped; arises from lateral epicondylar ridge, deep to short extensor. Its slender tendon passes under tendon of abductor pollicis longus and under a stout ligament (which is in position of extensor pollicis brevis). Insertion, second metacarpal near middle of radial surface.

*M. extensor carpi radialis brevis*.—In pocket gophers larger than the preceding; origin from lateral epicondylar ridge; insertion on middle of radial surface of third metacarpal.

*M. supinator*.—Arises by a tendon from radial collateral ligament of elbow joint. Large sesamoid bone in tendon in pocket gophers, similar to that in most muroid forms (Parsons, 1896). Inserts on oblique part of cranial border of radius, and on area between this and capitulum. In the other rodents examined, there is no sesamoid bone in the tendon of origin. The supinator does not have an ulnar origin in most rodents, nor in monotremes and insectivores; the condylar origin is probably primitive (cf. Leche, 1900).

*M. abductor pollicis longus*.—In rodents, as in most mammals, there is no extensor pollicis brevis. Abductor pollicis stout, arising from oblique part of cranial border of radius and from lateral fossa and body of ulna. Converges in bipennate manner to form a tendon. This passes superficially over extensores carpi radiales and through the most radial groove and compartment of wrist; inserts on abductor process of first metacarpal.

*M. extensor digitorum communis*.—Arises from lateral epicondyle of humerus. Divides into four parts; tendons pass through middle compartment under dorsal carpal ligament. On dorsum of hand, tendons separate and pass to four ulnar digits, united to each other by dense fascia near the metacarpophalangeal joints. Insertion partly on dorsal fascia, partly on bases of distal phalanges.

*M. extensor indicis et pollicis*.—Represents extensor indicis proprius and (perhaps) extensor pollicis longus, although there is some evidence to the contrary with respect to the latter (Curnow, 1876). Origin from lateral epicondyle and radial collateral ligament. Its slender tendon passes through middle compartment of wrist, deep to extensor communis tendons. On dorsum of manus it crosses over tendon of extensor carpi radialis brevis and divides into two slips. One joins tendon of common extensor of second digit, the other inserts on dorsum of pollex. In *Aplodontia*, *Citellus*, and *Sciurus* there is no slip to the pollex, and in these animals (as in most other rodents) origin is from the ulna.

*M. extensor digiti quinti proprius*.—Slender in pocket gophers. Origin, lateral epicondyle of humerus; diverges from common extensor near wrist; inserts on ulnar surface of second phalanx of fifth digit. In squirrels and in *Aplodontia* the tendon divides, inserting on the fourth and fifth digits. Insertion on the fourth digit is found in most rodents and is probably primitive (Parsons, 1894a, 1896; Leche, 1900).

*M. extensor carpi ulnaris*.—Arises from lateral epicondyle of humerus and from middle half of lateral ridge of ulna. Its tendon passes through a special groove and compartment on ulnar side of wrist; inserts on ulnar side of fifth metacarpal, near base.

#### FLEXOR SYSTEM

**Pectoral group** (figs. 13, 17, and 18). Supplied by the two anterior thoracic nerves, except for the subclavius which is supplied by a special nerve.

*M. ectopectoralis* (*pectoralis major*).<sup>2</sup>—Separable in pocket gophers, as in many other rodents, into a small superficial part and a larger deep one. Superficial muscle not completely distinct; arises from manubrium sterni and midventral line; inserts with deeper muscle on lateral ridge of humerus. Deep muscle takes origin from manubrium, sternebrae, and costal cartilages of true ribs; converges to a broad aponeurotic tendon; inserts on lateral ridge of humerus and on fascia of arm. In squirrels and *Aplodontia*, the superficial muscle is not separable. In rodents the clavicular part of the ectopectoral is absent (Parsons, 1894a, 1896).

*M. entopectoralis* (*pectoralis minor*, *pectoralis abdominalis*, and *cutaneus maximus*).

<sup>2</sup> Howell (1886: Anat. Record, 66:307) considers this muscle related to suprascapular muscles, rather than to pectoral group.

*M. pectoralis minor*.—Arises, in *Thomomys* and *Geomys*, from second to fourth sternbrae and from costal cartilages of second to fifth ribs—caudal part of origin aponeurotic. Inserts on coracoid process, dorsal to origin of coracobrachialis. Lander (1918) offers evidence that this attachment is primitive. In *Dipodomys*, pectoralis minor inserts partly on the head of the humerus, partly on the coracoid. This double insertion was found in *Citellus*, and Parsons (1896) describes a similar insertion in *Arvicola*. In *Aplodontia*, pectoralis minor inserts on the greater tubercle of humerus, whereas in *Sciurus* it attaches to the lateral

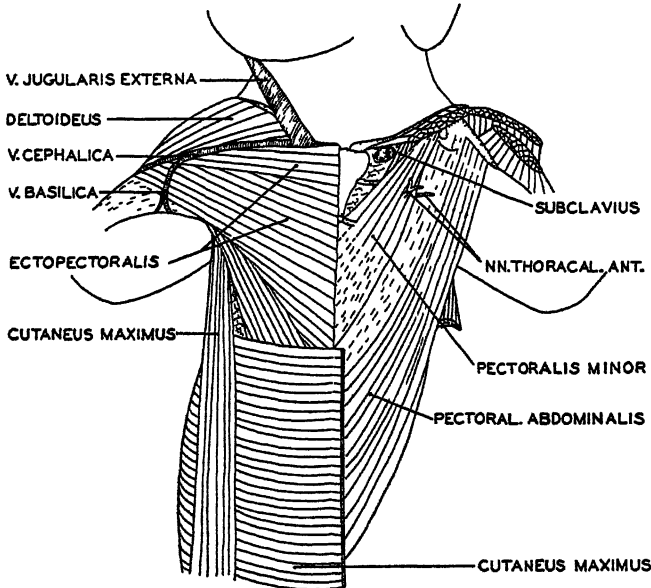


Fig. 18. Pectoral muscles (*Thomomys bulbivorus*),  $\times 1$ .

ridge. It is almost completely continuous with pectoralis abdominalis in squirrels and in *Aplodontia*; in pocket gophers the interval between the two muscles is closed by fascia.

*M. pectoralis abdominalis*.—In pocket gophers and in *Aplodontia*, arises from xiphisternum and midventral aponeurosis, in continuity with ectopectoral; runs obliquely, deep to ectopectoral; inserts on medial side of lateral ridge of humerus. In squirrels it attaches more distally on the humerus.

*M. cutaneus maximus* (fig. 18).—This name is preferable to the more common one, "panniculus carnosus," since the latter is used frequently to include the platysma (cf. Cunningham, 1927, p. 448). In pocket gophers, cutaneus maximus is divided into humeral and ventral parts. The former, corresponding to that of the rat (Langworthy, 1925), inserts on humerus near insertion of pectoralis abdominalis. Spreads out fan-wise over lateral body wall, running caudodorsal and then caudad. Converges over sacrum, attaching to fifth or sixth caudal vertebra and fascia of tail. In the axilla a straplike part separates from main part of muscle and runs caudad, nearly parallel with midventral line; in perineal region converges and joins dorsal part, attaching to tail. Ventral part resembles cutaneus maximus in the rabbit (Langworthy, 1925), arising from linea alba; blends with the humeral muscle over back and flanks. Both parts supplied by medial anterior thoracic nerve. In *Heteromys* (Parsons, 1896) the muscle is little differentiated from pectoralis abdominalis, from which it is apparently derived (cf. Langworthy, 1924, 1925). In *Aplodontia* and in *Citellus* this is also true. Apparently in pocket gophers the humeral part retains its primitive insertion on the humerus, while the origin has migrated from the midventral line to the skin. The reverse seems true of the ventral part; the primitive origin is retained, while the insertion has migrated to the skin.

*M. subclavius*.—Arises from first rib; inserts on deep surface of most of lateral half of clavicle.

**Flexor group of the arm** (figs. 15, 16, and 17). Supplied by the musculocutaneous nerve, except for some fibers of the brachialis which are innervated by the radial nerve.

*M. coracobrachialis*.—Two, possibly three, primitive parts of this muscle (Wood, 1876b) are present in pocket gophers. Origin by a tendon, common to it and short head of biceps, from tip of coracoid process. Short part separates from rest of muscle near head of humerus; inserts on humerus, medioproximal to insertions of teres major and latissimus dorsi. Long part (possibly middle and long parts fused) inserts on medial ridge from insertion of teres major to medial epicondyle. The musculocutaneous nerve passes between the two parts of the muscle.

The description given above is suitable for *M. coracobrachialis* in the two genera of squirrels, but in *Aplodontia* the short portion inserts partly on the neck of the humerus and partly on the longer portion.

*M. biceps brachii*.—In pocket gophers completely divided into two muscles. *Caput breve*: origin with coracobrachialis from coracoid process; insertion, tuberosity of radius. *Caput longum* much stouter; arises from supraglenoid tuberosity; its tendon lies in intertubercular groove; inserts on tuberosity of ulna, immediately distal to coronoid process. A well-developed short head was found in *Citellus richardsonii*, although it is said to be absent in *Citellus mexicanus* (Parsons, 1894a) and in *Citellus beecheyi* (Holliger, 1916). In this animal (*C. richardsonii*), in *Sciurus*, and in *Aplodontia*, two heads of biceps unite and insert on tuberosity of radius. Some fibers, in *Aplodontia*, insert on ulna also. The biceps brachii probably represents a fusion of two distinct muscles (Leche, 1900) of the premammalian forms, but the separation of these two parts in pocket gophers and in *Dipodomys* (Howell, 1932) is doubtless secondary.

*M. brachialis*.—Large, with two imperfectly separated heads. One arises from lateral surface of humerus and from base of greater tubercle; other takes origin from cephalic surface, medial to deltoid ridge; the two unite in cubital fossa. Insertion with long head of biceps on ulna. The medial part is rudimentary in the squirrels and *Aplodontia*.

**Flexor group of the forearm** (fig. 17). The deep flexor of the digits contains several parts that in man are associated with the superficial flexor (McMurrich, 1902b). The median and ulnar nerves supply the flexors of the forearm; however, while valuable in the identification of individual muscles, they have less importance in indicating derivation and phylogeny.

*M. epitrochleo-anconeus*.—Found in most mammals except man. It is invariably supplied by the ulnar nerve (Leche, 1900; McMurrich, 1903; Howell and Straus, 1931), although several authors considered it a part of the triceps. In pocket gophers short and relatively stout; arises from medial epicondyle; passes superficially over ulnar nerve; inserts on medial surface of olecranon.

*M. flexor carpi ulnaris*.—In pocket gophers humeral head absent; arises from caudomedial surface of olecranon. Large and pennate. Tendon forms on medial border; inserts on pisiform. Fascia continues distad from pisiform, to secondary insertions on fourth and fifth metacarpals. In both genera of squirrels, in most rodents (Parsons, 1894a, 1896), and in many mammals of other orders (Leche, 1900) the epicondylar head is present; probably the primitive condition. In *Aplodontia* the epicondylar head arises from the fascia of *M. epitrochleo-anconeus*. Supplied, in all, by ulnar nerve.

*M. palmaris longus*.—Larger than usual in pocket gophers and in *Aplodontia*, whereas almost vestigial in squirrels. Arises from medial epicondyle; tendon develops near middle of forearm; inserts on falciform bone and fascia of hand. It attaches to the pisiform also in *Aplodontia*; in squirrels the insertion is largely into fascia.

*M. flexor carpi radialis*.—Arises from medial epicondyle of humerus. Tendon runs along radius, bound by ligament near distal end. Inserts on radial sides of second and third metacarpals; additional attachment to transverse metacarpal ligament. In *Citellus* and *Aplodontia* the latter insertion is absent.

*M. pronator teres*.—Stout; origin, medial epicondyle; insertion, oblique part of cephalic border of radius and area between this and capitulum. Larger in *Geomys* than in *Thomomys*,



and even larger in the squirrels and *Aplodontia*. The ulnar head is absent in rodents as in most mammals except man (cf. Macalister, 1869).

*M. flexor digitorum sublimis*.—Corresponds in pocket gophers, as in the mouse, to primitive condylo-ulnar flexor (McMurrich, 1902b). Arises from medial epicondyle; inserts on middle three digits, on second phalanges; tendons perforated by those of deep flexor as usual. Belly of superficial flexor muscle complex—three bipennate muscles closely bound together. In *Geomys*, muscle inserting on third digit much the largest, but the three are subequal in *Thomomys*. In squirrels the most ulnar of the tendons divides and inserts on the fourth and fifth digits. In *Aplodontia* there is a fourth muscle belly as well as this extra tendon. This may signify a contribution from *M. palmaris longus*, as in the cat (McMurrich, 1902b). Superficial flexor and the three preceding muscles supplied by median nerve.

*M. flexor digitorum profundus*.—Four muscles compose this complex flexor in pocket gophers: the ulnar, central, condyloradial, and radial heads (cf. Windle, 1890). Ulnar head arises from proximal three-quarters of caudal and medial surfaces of ulna; the largest of the several parts. Slender central head and larger condyloradial portion take origin from medial epicondyle, while radial head arises from proximal third of radius. The last is small; it unites with condyloradial muscle to form a common tendon. This and the other two tendons unite at wrist. On volar surface of manus this common tendon divides into five; insertion, bases of terminal phalanges of all digits. Deep flexor proportionately larger in *Geomys* than in *Thomomys*, but relations similar. In *Citellus*, part of the condyloradial muscle remains independent; inserts on the pollex. Ulnar head supplied by ulnar nerve, but rest of deep flexor by median.

*M. pronator quadratus*.—Small, thin, running almost transversely; arises from ulna for most of distal third; inserts on corresponding part of radius. Continuous with interosseous membrane, probably a remnant of an extensive interosseous muscle. In *Sciurus* it is reduced in size, but in the other rodents examined it is much as described above.

**Flexor group of the manus.** According to McMurrich (1903), a number of these muscles have united with the tendons of the long flexor muscles and form, in mammals, the distal extensions of these. Fewer muscles are identifiable in pocket gophers than in most mammals, the volar surface being covered by dense fascia. The following muscles are well developed.

*M. abductor pollicis brevis*.—Arises from distal surface of falciform near base; inserts on base of proximal phalanx of pollex on radial side. In *Aplodontia* there are also a small adductor and an opponens pollicis. In *Citellus*, however, muscles of thumb are largely fascial.

*M. abductor digiti quinti*.—Origin, pisiform; insertion, ulnar side of proximal phalanx of fifth digit. In *Aplodontia* there is also an adductor digiti quinti, but I was unable to find this in the other forms examined.

*Mm. lumbricales*.—Arise from deep flexor tendon; insert on metacarpophalangeal joints of the four ulnar digits. In pocket gophers the muscle of the fifth digit is largest and most constant.

*Mm. Interossei*.—Six in pocket gophers, relatively large; associated with three middle digits. Origin, volar surface of metacarpals; insertion, sesamoid bones of metacarpophalangeal joints. There are eight interossei in *Aplodontia* and in *Citellus*.

## MUSCLES OF THE PELVIC GIRDLE AND LIMB

### EXTENSOR SYSTEM

**Iliacus group** (figs. 19, 20, and 21). Analogous to suprascapular group in the forelimb. Some fibers of *M. pectineus* are supplied by the obturator nerve and are probably derived from the adductor group. The rest of pectineus and the other members of the group are supplied by branches of the femoral nerve.

*M. iliacus*.—In pocket gophers large and quadrilateral. Arises from iliac fossa and from transverse process of last lumbar vertebra; inserts on lesser trochanter, deep to psoas major and on shaft of femur for several millimeters distad. Femoral nerve emerges between iliacus and psoas major, but since the latter muscle migrates from the ilium to the spinal column during ontogenetic development (Lewis, 1910), its relationship to the femoral nerve is not very significant.

In squirrels and in *Apiodontia* it would appear, from the evidences of insertion and relation to the femoral nerve, that the iliacus had divided, one part obtaining a large origin from the lumbar vertebrae, even more extensive than that of psoas major. Alezais (1900) considers this portion to be part of psoas major, however, and this conclusion may be correct.

*M. psoas major*.—Origin, in *Thomomys*, bodies and transverse processes of last two or three lumbar vertebrae and first two or three sacrals, and ventral border of ilium. Bipennate in *Geomys*; less extensive in origin. Inserts on lesser trochanter.

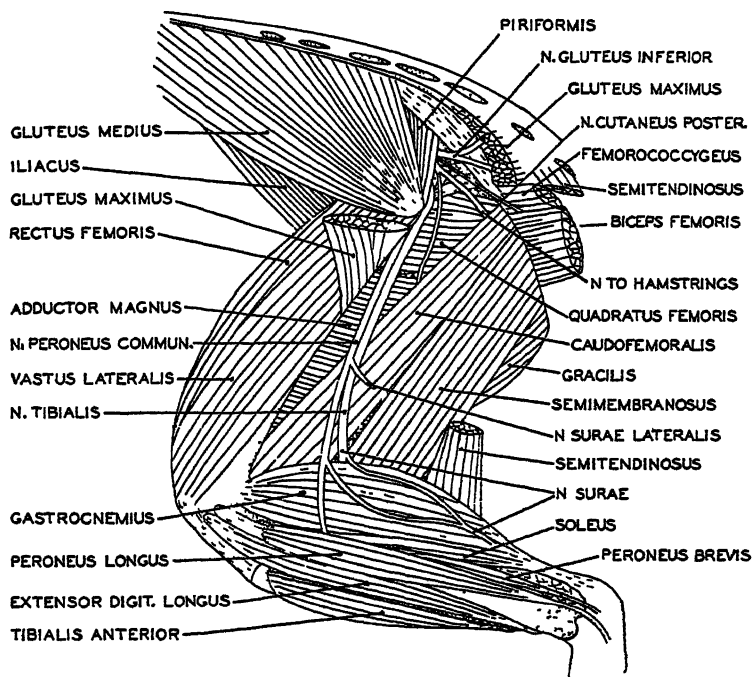


Fig. 19. Lateral muscles of hip and hind limb (*Thomomys bulbivorus*),  $\times 1\frac{1}{4}$ .

*M. pectineus*.—Arises from ventral border of pubis, ventral to acetabulum and caudal to iliopectineal eminence. In *Thomomys* it is complex—several tendons form; but in other rodents, including *Geomys*, it is simple. Inserts into shaft of femur, distal and slightly caudal to lesser trochanter.

**Gluteal group** (figs. 19 and 20). Analogous to latissimus-subscapular muscles of forelimb. This would agree with Flower's interpretation (1870) of the surfaces of the ilium and scapula, but would not involve the rotation of the girdles, the muscles having apparently migrated. The gluteal muscles are in two layers, a lateral and a medial.

Lateral layer, or superficial gluteal muscles, include tensor fasciae latae, gluteus maximus, femorococcygeus, and tenuissimus. The first is supplied by terminal branches of the superior gluteal nerve; tenuissimus, by a branch of the common peroneal nerve; the others, by the inferior gluteal nerve. The two gluteal nerves are derived from a common nerve (Apleton, 1928) and both are intimately related to the common peroneal, so these differences in innervation are not of great importance.

*M. tensor fasciae latae*.—Caudally completely continuous with gluteus maximus in origin and insertion. Arises from crest of ilium and from aponeurosis over gluteus medius. Inserts into poorly developed lateral fascia and on cranial and distal part of lateral ridge of femur. In pocket gophers it is restricted to lateral side of thigh; in the other rodents it is much larger, with a well-developed medial part, the whole supplied by the superior gluteal nerve. Howell (1926, 1932) and Parsons (1894a, 1896) found this medial part in many rodents; always supplied by the superior gluteal nerve. In squirrels, besides this medial part, there is

a straplike sartorius. These facts agree with Howell's conclusion that in many rodents sartorius does not fuse with tensor fasciae latae, but is lost.

*M. gluteus maximus*.—Thin, broad. Arises from spines of third to fifth sacral vertebrae and from aponeurosis covering gluteus medius. Stoutest caudal part forms tendon which inserts into gluteal tuberosity. Rest of muscle inserts by aponeurosis on lateral ridge of femur. In squirrels and in *Aplodontia* it is practically inseparable from *M. femorococcygeus*.

*M. femorococcygeus* (Leche, 1883).—Usually called "caudofemoralis," but this name was given to an entirely different muscle, one of the flexor group (cf. Appleton, 1928). It has

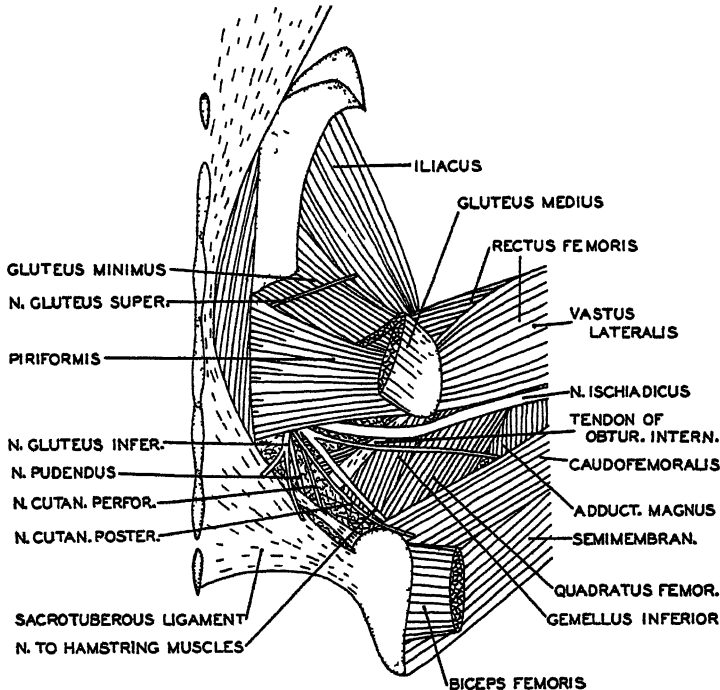


Fig. 20. Deep muscles of hip joint (*Thomomys bulbivorus*),  $\times 1\frac{1}{2}$ .

also been called "biceps femoris anticus" in rodents, but while it may fuse with *M. biceps* (as in some ungulates, Kolesnikow, 1933), it is primitively distinct and is related to *gluteus maximus*. In squirrels and in *Aplodontia*, *femorococcygeus* arises from transverse processes of first two caudal vertebrae (last two sacral vertebrae in *Aplodontia*); inserts on lateral surface of femur, proximal to condyles. In *Dipodomys*, origin aponeurotic from spines of last few sacral vertebrae and by fleshy fibers from their transverse processes. Some fibers which pass over the ischial tuberosity attach to it. In *Thomomys* and *Geomys* the proximal part has become a stout sacrotuberous ligament, extending from spines of last several sacral and first caudal vertebrae to dorsal part of ischial tuberosity. The muscular part of *femorococcygeus* continues distad from this ligament, arising partly from the ligament, partly from the ischial tuberosity; inserts on patella and most distal part of femur. This insertion is like that in most murid forms (Parsons, 1896) and seems to be a secondary extension of the muscle, since its primitive insertion is on the proximal half of the femur (Appleton, 1928).

The sacrotuberous ligament has apparently developed in similar ways, but independently, in a number of mammals (cf. Appleton, 1926).

*M. tenuissimus*.—Absent in most specimens of *Thomomys*, but in two individuals (one *bulbivorus* and one *bottae*) there was a slender rudiment; absent in *Geomys*. In *Dipodomys* (Howell, 1932) and in *Citellus* it is present, but vestigial; it is relatively large and apparently functional in *Sciurus* and *Aplodontia*.

*Medial layer*.—Supplied by the superior gluteal nerve. In some specimens, however, the nerve to piriformis appears to arise independently, associated with the superior gluteal nerve.

*M. gluteus medius*.—In pocket gophers, two parts. Superficial fibers take origin from spines of first four sacral vertebrae, from lumbodorsal fascia, and from crest of ilium and its spine. Deeper layer separated from superficial except along ventrolateral margin and in insertion; arises from most of gluteal fossa of ilium, closely associated with piriformis. In *Aplodontia*, *M. piriformis* is quite inseparable from *M. gluteus medius*, and the latter muscle is less divided. Somewhat intermediate conditions are found in the squirrels.

*M. piriformis*.—In pocket gophers closely associated with deep layer of *gluteus medius*. Arises from transverse processes of second, third, and fourth sacral vertebrae. Inserts with *gluteus medius* on greater trochanter. In *Aplodontia*, part of the origin has migrated to the ventral surface of the sacrum. Piriformis appears to have been derived from the *gluteus medius* in rodents, as in other mammals (cf. Appleton, 1928).

*M. gluteus minimus*.—Separated by superior gluteal nerve and vessels from the preceding. Small in pocket gophers; arises from caudal and lateral part of gluteal fossa and from iliac ridge. Inserts with *gluteus medius* on craniomedial surface of greater trochanter. In squirrels, *gluteus minimus* has invaded the iliac fossa; this is carried to an extreme in the mureids. In *Aplodontia* it is restricted to the gluteal fossa and iliac spine. This is also the condition in *Dipodomys* (Howell, 1932). In all rodents examined, *M. scansorius* is continuous with *gluteus minimus*; fibers which arise from the iliac ridge probably represent that muscle.

**Quadriceps femoris group** (figs. 19, 20, and 21). Analogous to the triceps group of the brachium. The femoral nerve innervates these muscles.

*M. rectus femoris*.—In *Thomomys*, two heads of rectus femoris separate but close together. Reflected head arises from roughened area craniodorsal to acetabulum; straight head takes origin from tuberosity at acetabular end of iliac ridge. Belly compressed laterally. In *Geomys*, two heads united, as in *Dipodomys* (Howell, 1932); single tendon originates from strong tuberosity in front of acetabulum. In squirrels the two heads are distinct, particularly in *Sciurus*; in *Aplodontia*, although separate, they are close together.

*M. vastus lateralis*.—Largest muscle of the group, arising from greater trochanter, from cephalic surface of lateral ridge, and from laterocranial surface of femur. Inserts on aponeurosis of rectus and on laterodorsal surface of patella.

*M. vastus medialis*, *M. vastus intermedius*, et *M. articularis genu*.—In pocket gophers these muscles form a single mass, difficult to separate from vastus lateralis. Origin, from cranial and medial surfaces of femur.

The rectus and vasti muscles unite to form a large extensor tendon inserting on the patella and secondarily, by the patellar tendon, on the tuberosity of the tibia.

*M. sartorius*.—Absent in pocket gophers, as in many rodents, including *Aplodontia*. In squirrels, straplike; arises from inguinal ligament (cf. Parsons, 1894a), as in the rabbit (Bensley, 1926). Contrary to Parsons' statement, this muscle is supplied by the femoral nerve, as is sartorius in man. Inserts on cranial crest of tibia with gracilis.

**Tibial extensor group** (fig. 19). Analogous to radial and long extensors of the forearm, although represented by only three muscles. Supplied by the deep peroneal nerve.

*M. extensor digitorum longus*.—Arises from a depression near lateral lip of patellar groove on epicondyle of femur (see fig. 8) and from fibular collateral ligament. In lower quarter of leg four tendons form; pass under dense ligamentum transversum cruris. (This ligament attached to cranial surface of tibia and to lateral malleolus.) Tendons pass through pulleylike ligamentous loop, attached to calcaneus (such as Keith, 1894a, described in lower primates); tendons united by fascial bands, much as tendons of comparable muscle in forelimb. Insertion, terminal phalanges of the four fibular digits, with some fascial attachment to each phalanx and to heads of metatarsals.

*M. extensor hallucis longus*.—Slender; origin from interosseous membrane and fascia of adjacent muscles. Tendon runs with that of tibialis anterior in a groove on cranial surface of tibia. Inserts on terminal phalanx of hallux. The intimate relationship with tibialis ante-

rior throughout the entire length of the latter might indicate that both have been derived from a single muscle, or extensor hallucis may have migrated along tibialis anterior.

*M. tibialis anterior*.—Large; in pocket gophers and in *Aplodontia* it arises from lateral condyle and proximal half of body of tibia; inserts on first cuneiform and base of first metatarsal. In squirrels, the insertion is restricted to the first cuneiform.

**Peroneal group** (fig. 19). It appears from the work of Ruge (1878) that the muscular branches which supply the peroneal muscles are usually associated with both the deep and superficial branches of the common peroneal nerve, and that the fibers associated with each branch are not always equivalent. Thus in pocket gophers the branch to peroneus longus arises from the deep ramus, whereas the branches to the other peroneal muscles of the leg come off from the superficial ramus. The members of the extensor brevis in the foot are supplied by the deep peroneal nerve. The peroneal muscles appear analogous to extensor carpi ulnaris, extensor indicis et pollicis, and extensor digiti quinti of the forearm.

*M. peroneus longus*.—Origin, lateral and cranial surfaces of head of fibula. Slender tendon, in pocket gophers (and muroid rodents, Parsons, 1896), passes through special groove in lateral malleolus (see fig. 9); continues through groove in trochlear process of calcaneus and across tarsus, deep to flexor tendons, to insert on first cuneiform and first metatarsal bones. In some specimens, an additional attachment to third cuneiform. In squirrels and *Aplodontia* the tendon passes behind the lateral malleolus with the other peroneal muscles. Ruge (1878) concluded that the primitive insertion of peroneus longus was the tuberosity of the fifth metatarsal. *Sciurus* exhibits this attachment besides those described in pocket gophers, but neither *Citellus* nor *Aplodontia* do.

*M. peroneus brevis*.—Stoutest of the group. Arises from cranial surface of fibula, from interosseous membrane, and from part of tibiofibula. Tendon passes behind and under lateral malleolus; runs over trochlear process of calcaneus; inserts on tuberosity of fifth metatarsal. Closely associated with extensor brevis of fifth digit.

*Mm. extensores digitorum breves*.—Ruge (1878) concluded that these muscles belong with the peroneal group. In rodents there are four muscles: two arise from the fibula; the other two arise from the calcaneus. The two elements which take origin from the fibula, "peroneus digiti quinti" and "peroneus digiti quarti," are supplied by the superficial peroneal nerve; the slips which arise from the calcaneus are supplied by the deep peroneal nerve. Extensor brevis of fifth digit arises from caudal surface of fibula and from fascia of adjacent muscles; inserts by slender tendon on distal end of fifth metatarsal and on proximal ends of first and second phalanges. Extensor brevis of fourth digit takes origin from distal half of fibula on lateral surface and from fascia of other peroneal muscles; tendon inserts on dorsolateral surface of metatarsal of fourth digit and on all its phalanges, uniting with long extensor over middle phalanx. Other two muscles attach to second and third digits; arise from dorsal surface of calcaneus and join tendons of long extensor over metatarsal bones, near heads of these.

#### FLEXOR SYSTEM

**Adductor group** (fig. 21). Innervated by the obturator nerve. Functionally these muscles may be compared with the pectoral group of the forelimb, whether or not they are serially homologous. As Appleton (1922) has shown, the best guide to the homology of the individual adductor muscles is their topographical relations to the branches of the obturator nerve, to each other, and to adjacent muscles. In man the nerve to the gracilis passes between adductor longus and adductor brevis, the latter lying caudal to the nerve. The branch of the obturator nerve supplying adductor magnus passes between that muscle and adductor brevis, the latter muscle being situated medially and cranially in respect to the nerve. In all the rodents examined, including *Dipodomys*, *Eutamias*, and *Neotoma*, besides the other five genera, there are muscles with topographical relationships to these nerves similar to those described above. These muscles agree with the respective muscles in man in their origins, their relations to one another, and their relations to neighboring muscles. Consequently, in spite of differences in size and insertion, I conclude that the muscles which exhibit these similar relationships are homologous with the respective muscles in man.

*M. gracilis*.—In a few specimens of *Thomomys* the two parts of this muscle, found by Howell (1926, 1932) in some other rodents, were present. In the majority of specimens, however, only the caudal part was found, and this was the only part found in the specimens of *Geomys*. Caudal part arises from ventral margin of hip bone, caudal to obturator foramen; inserts into anterior surface of tibia, proximal to semitendinosus (see fig. 21). Cranial part, when present, arises from ventral margin of hip bone in front of other part; inserts by aponeurosis into fascia over knee-joint. Caudal muscle narrower and thicker than cranial one. In squirrels and *Aplodontia*, *M. gracilis* is wider, single; it probably represents only the caudal element. It inserts more proximally on the tibia in these forms than in pocket gophers.

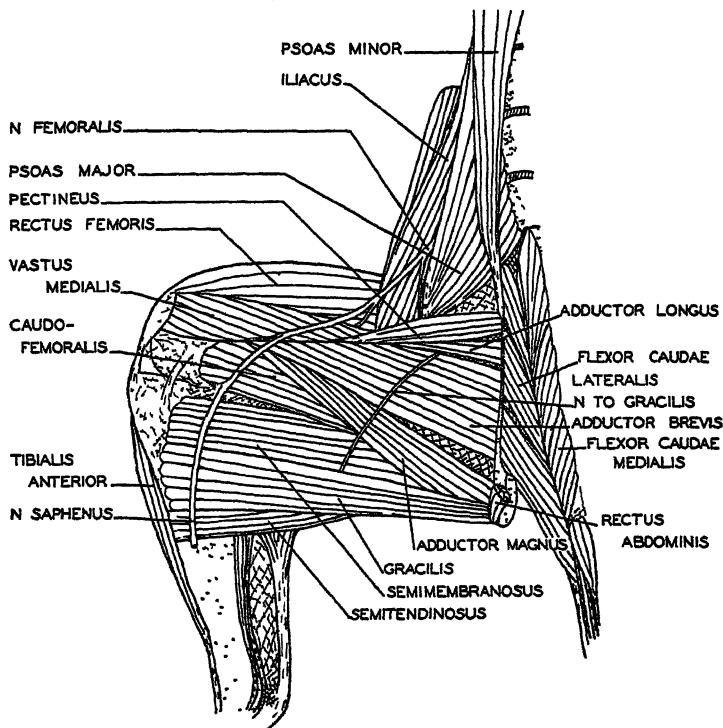


Fig. 21. Medial muscles of hip and hind limb (*Thomomys talpivorus*),  $\times 1$ .

The double condition of the gracilis may be primitive (cf. Leche, 1900). At least, in pocket gophers the loss of the cranial muscle appears to be secondary, since it is present in *Dipodomys* and in some specimens of *Thomomys*.

*M. adductor longus*.—Shortest of group, as often in mammals other than primates. Most medial and cranial of adductors, in rodents as in man; lies caudal to pectineus on medial side of thigh. Slender in pocket gophers; arises from ventral margin of pubis immediately caudal to pectineus and craniomedial to adductor brevis. Inserts by a tendon into medial surface of femur near middle, in some specimens uniting with pectineus. It agrees with this description in the other rodents examined, except in *Sciurus*, where it is larger and partly fused with adductor brevis.

*M. adductor brevis*.—Middle of three adductors. Origin, ventral margin of hip bone ventral to obturator foramen, between origins of gracilis and obturator externus, craniomedial to adductor magnus and caudodorsal to adductor longus, similar to origin of adductor brevis in man. In pocket gophers and in squirrels it inserts between adductor magnus and adductor longus, attaching to middle half of femur on caudomedial surface. The origin is similar in all rodents examined and the insertion retains the same relationships, but it is greatly increased in extent in *Dipodomys*, *Neotoma*, *Rattus*, and *Aplodontia*, reaching distad to the epicondyle.

Alezais (1900) describes this muscle as part of the great adductor in *Sciurus vulgaris* and *Rattus norvegicus*. Howell (1926) calls it in *Neotoma* "adductor magnus," and (1932) in *Dipodomys* "adductor longus primus." That it is not adductor magnus is indicated by the fact that it is the middle of the three adductor muscles. Also its relations at its origin, described above, do not accord with those of the human adductor magnus. It is, moreover, bounded cranially by the nerve to gracilis (see fig. 21), and caudolaterally by the nerve to the more lateral adductor. These relations further differentiate it from adductor longus.

*M. adductor magnus*.—The obturator part of the great adductor is separate from the sciatic element (see *M. caudofemoralis*, p. 127), although closely approximated to it, a common condition in mammals (Leche, 1900; Parsons, 1892). Adductor magnus is the most lateral of the adductors; situated ventrally in relation to quadratus femoris, dorsolaterally in relation to gracilis and part of adductor brevis, craniomedially in relation to semimembranosus, and medially in relation to caudofemoralis. In the geomyoid forms, adductor minimus is distinct, although this is less evident in *Geomys* than in *Thomomys* and *Dipodomys*.

*M. adductor minimus*.—Arises from hip bone, deep to adductor brevis and ventral to quadratus. Runs almost horizontally, in contact with adductor magnus proper, to insert on caudal surface of lateral ridge of femur. Insertion continuous with rest of adductor magnus and with quadratus femoris. It is thus similar to that of the adductor minimus element in man.

*M. adductor magnus proprius*.—Arises from quadrilateral area between obturator foramen and ventral tuberosity of ischium; bounded cranially by obturator externus and adductor minimus, dorsally by quadratus femoris, caudally by semimembranosus, ventrally by gracilis and adductor brevis. Inserts on lateral ridge of femur, distal to insertion of adductor minimus, extending almost to epicondyle. These relationships are similar to those of the corresponding part of great adductor in man.

In *Dipodomys*, *Citellus*, and *Aplodontia* the two parts of adductor magnus are as described above. Howell (1932) considers the muscle I have described as adductor minimus to be adductor brevis. It is, however, caudolateral to the branch of the obturator nerve supplying it and adductor magnus proprius; and all its relations are so similar to those of the adductor minimus element in man that it seems unlikely to be other than homologous with that muscle. In *Rattus* and *Neotoma*, adductor magnus is undivided and reduced in size. In the latter animal, Howell (1926) called it "adductor brevis," but it is the most lateral of the group. In spite of its reduced insertion, restricted to the caudal surface of the lateral ridge for the middle half of the femur, its relationships to nerves and muscles are as described above. In *Sciurus*, adductor magnus is divided into three parts, all in the one plane and continuous in insertion. The adductor minimus arises from the symphyseal region; inserts on the caudal surface of the third trochanter. The middle part arises by a tendon from the ventral tuberosity of the ischium; inserts on the middle third of the femur. The third part arises from the descending ramus of the ischium; inserts on the rest of the caudolateral surface of the shaft of the femur. (See also Alezais, 1900).

*M. obturator externus*.—Origin from borders of obturator foramen and from obturator membrane; insertion by tendon into deep trochanteric fossa.

**Ischiotrochanteric group** (figs. 19 and 20). Two gemelli muscles and quadratus femoris are, in pocket gophers, supplied by a branch of the tibial nerve. The nerve to obturator internus supplies only that muscle. The muscles of this group are intimately associated in their insertions. This group is analogous to the coracobrachialis muscle of the brachium, since both are short flexors.

*M. obturator internus*.—Origin from a well-marked area on pelvic surface of ischium, caudal to obturator foramen. Long tendon passes over lesser sciatic notch; joined by gemelli; inserts into trochanteric fossa and trochanteric crest. Large in *Aplodontia*; origin from almost entire pelvic surface of hip bone.

*M. gemellus superior*.—Arises from gluteal surface of spine of ischium and from dorsal border of ischium in front of this. Inserts on tendon of obturator internus and in trochanteric fossa, in front of the tendon. The muscle described under this name in *Neotoma* and

*Dipodomys* by Howell (1926, 1932), while apparently homologous to the muscle so designated in the cat by Reighard and Jennings (1930), is probably not homologous to that in man, judging from its relationships and from the fact that there is another muscle with the attachments and relations of gemellus superior. Parsons (1894a, 1896) found the gemelli in rodents similar to those in man.

*M. gemellus inferior*.—Arises from cranial surface of dorsal ischial tuberosity. Inserts on tendon of obturator internus.

*M. quadratus femoris*.—Large in pocket gophers, taking origin from lateral surface of ischium between dorsal and ventral ischial tuberosities and from the former tuberosity deep to the hamstring muscles. The part arising from the tuberosity is tendinous and its insertion fleshy, whereas the reverse is true of the rest of the muscle. Insertion, caudal surface of lesser trochanter, trochanteric crest, and adjacent, flattened caudal surface of femur. Conditions are very like those described by Howell (1932) in the kangaroo rat. Smaller in the other forms, especially *Aplodontia*, but relationships similar.

**Hamstring group** (figs. 19, 20, and 21). The hamstring muscles are innervated by a special branch of the tibial nerve. They are analogous to biceps brachii, but form the largest muscle group in the body.

*M. caudofemoralis*.—Origin, dorsal margin of ischium; insertion, medial epicondyle of femur. Usually considered part of the semimembranosus which has become independent, the presemimembranosus. Other authors, recognizing the morphological relation to part of adductor magnus in man, have called it the "ischiocondylar" part of that muscle.

Parsons (1894a) found all intermediate stages in rodents between union of this muscle with semimembranosus and with adductor magnus. Since the caudofemoralis is differentiated in the lower tetrapods, both of these unions should be considered secondary and Leche's (1900) conclusions as to the origin of the sciatic part of the great adductor, that it was derived from a part of the semimembranosus muscle, be modified (cf. Appleton, 1928; Hill, 1934).

In squirrels and in *Aplodontia*, *M. caudofemoralis* is partly divided, one portion inserting on the caudal surface of the distal third of the femur, the rest attaching to the medial epicondyle.

*M. semimembranosus*.—Origin, caudal border of ischium and ventral ischial tuberosity. Inserts by flat tendon into mediocranial surface of tibia near its head.

*M. semitendinosus*.—Arises, in pocket gophers, from spines of last sacral and first caudal vertebrae, from sacrotuberous ligament, and from dorsal tuberosity of ischium. Relatively smaller in *Geomys* than in *Thomomys*. Caudal and ischial heads are closely united. A well-marked inscription is present near the middle, such as Forster (1918) found in many mammals. This author considers the inscription to represent the insertion of the caudal head (flexor cruris dorsalis of Appleton, 1928) on the rest of the muscle. In squirrels and *Aplodontia*, where the ischial and spinal heads are more distinct, appearance confirms his thesis. The flat tendon of semitendinosus in pocket gophers and in *Aplodontia* inserts on the mediocranial surface of the tibia near the middle (see fig. 9). Insertion is nearer the knee joint in squirrels.

*M. biceps femoris*.—Only long head of biceps present as such. Arises from dorsal ischial tuberosity, superficial to caudofemoralis. Inserts into dense fascia lata of leg and, by semicircular tendon, into tendo calcaneus. Also attaches to lateral surface of head of tibia. There is no semicircular tendon in the insertion in the squirrels and *Aplodontia*, and in the latter the deeper fibers form a narrow muscle inserting on the capsule of the knee joint. In these animals the large lateral sural nerve pierces the biceps; in pocket gophers it passes between the biceps and femorococcygeus.

**Flexor group of the leg** (fig. 19). Supplied by the tibial nerve, except quadratus plantae which is innervated by the lateral plantar nerve, a branch of the tibial.

*M. gastrocnemius*.—Lateral and medial heads separate. Former takes origin from lateral epicondyle of femur (see fig. 8) by a tendon containing a sesamoid bone. Larger medial head arises from medial epicondyle (see fig. 8); its tendon of origin likewise contains a sesamoid bone. Tendons of insertion of the two muscles unite (separable with little difficulty,



however) and, together with tendon of soleus, form tendo calcaneus. This inserts on tuberosity of calcaneus. Twisted in a spiral manner as Parsons (1894b) described in other mammals.

*M. plantaris*.—Belongs to the superficial layer of flexors with *M. gastrocnemius* (McMurrich, 1904). Arises with lateral head of gastrocnemius from lateral epicondyle. Relatively large in pocket gophers. Stout tendon emerges from sheath formed by tendo calcaneus, passes to medial side of this and to plantar aspect of foot; divided into stout tendon to middle digit and more slender one to fourth, both perforated by long flexor tendons. Five slips in *Citellus* and in *Aplodontia*; in the former these insert on all digits, but in the latter they insert only on the four fibular digits and on the plantar sesamoid; insertion, in all slips, on the bases of the second phalanges. From this, and from the perforation, it seems probable that the plantaris tendon has fused with *Mm. flexores breves* as in many other rodents (cf. Howell, 1932). However, in pocket gophers, flexor brevis of second digit remains distinct. The wood rat (Howell, 1926) exhibits an intermediate stage; muscular fibers are present in the plantaris tendon. This appears to be the case in the slip attaching to the fifth digit in *Aplodontia*.

*M. soleus*.—Spindle-shaped; arises from caudal surface of head of fibula; unites with tendons of gastrocnemius; with them, inserts on heel bone. Larger in squirrels and *Aplodontia* than in pocket gophers, but relations similar.

*M. popliteus*.—Origin, lateral epicondyle of femur (see fig. 8), deep to fibular collateral ligament. Fan-shaped, expanding to insert on proximal three-eighths of medial border of tibia. No sesamoid bone in tendon of origin in the five genera examined.

*M. flexor digitorum tibialis*.—This name and that of "flexor digitorum fibularis" were proposed by Schulze (1866) to replace "flexor digitorum longus" and "flexor hallucis longus" respectively; he has been generally followed by comparative anatomists, since in most mammals the insertions of these muscles differ from insertions in primates. In pocket gophers, flexor tibialis takes origin from medial ridge of tibia, intimately associated with *M. popliteus*, medial fibers of which seem continuous with those of flexor tibialis. Slender tendon passes over medial malleolus in special groove (see fig. 9), as in muroid rodents; divides into two tendons. One inserts on base of first metatarsal, contains small sesamoid bone. In *Thomomys*, insertion on tibial surface of metatarsal; in *Geomys*, on plantar aspect. Fibers attach to medial tarsal bone and first cuneiform. Other tendon unites with that of flexor fibularis, as in *Heteromys* (Parsons, 1896). Flexor tibialis and flexor fibularis are separate in squirrels and in *Aplodontia*; tendon of former muscle lies in same groove and fascial sheath as tibialis posterior.

These conditions agree with those recorded by Dobson (1882) in *Thomomys talpoides* and in *Sciurus vulgaris*. It cannot be maintained, however, that the union of the flexor tendons is indicative of hystricomorph affinities. Rather this is the primitive condition (as he himself considers elsewhere) and consequently is likely to have been retained in various groups independently. It does, however, have phylogenetic significance, since it is fairly constant within smaller groups, such as families. I cannot agree with Dobson in a later paper (1885) in which he concludes that the separation of the tendons is a result of a fossorial habit, since the tendons are united in pocket gophers and the Bathyergidae (extremely adapted to a fossorial life), whereas in squirrels and most mice they are not.

*M. tibialis posterior*.—Apparently closely related morphologically to flexor tibialis (cf. Dobson, 1882). Two heads: one arises from caudal fossa of tibia, deep and caudal to insertion of popliteus; one from medial surface of head of fibula and fascia of flexor fibularis. Tendon formed in lower half of leg; passes over medial malleolus; inserts on medial tarsal bone.

*M. flexor digitorum fibularis*.—Large; origin, tibia and fibula and interosseous membrane for proximal two-thirds of leg. Fibers from tibia arise from medial side of interosseous border and adjacent caudal fossa. Fibular part originates from tibial and caudal surfaces of fibula. It passes through wide groove on caudal surface of tibiofibula between malleoli, and under sustentaculum tali of calcaneus. Divides on plantar surface of foot; tendons insert on

distal phalanges of five digits. In pocket gophers joined on the sole, before it divides, by tendon of flexor fibularis.

*M. quadratus plantae*.—McMurrich (1904) considers this one of the crural flexors, secondarily migrated to the foot. In pocket gophers largely fascial; a few muscle fibers arise from medial surface of calcaneus and insert on tendon of flexor fibularis.

**Flexor group of the pes.** Better developed than that of palm. The terminal branches of the tibial nerve, the lateral and medial plantar nerves, supply the several muscles, but the innervation of each muscle was not determined. The following muscles were found in the specimens dissected:

*M. flexor digitorum brevis*.—One slip remains independent in pocket gophers, the one inserting on the second digit, the others having apparently fused with the plantaris. The independent slip, somewhat flattened, arises from deep surface of plantaris tendon. Its slender tendon inserts on second phalanx of second digit, perforated by long flexor tendon to that digit. In squirrels the short flexors are in two layers; the superficial slips fuse with the plantaris tendon completely; the deep layer consists of two muscles which arise from the long flexor tendon (much as in mouse and cat, McMurrich, 1907). These insert on tendons of plantaris which attach to second and third digits. The deep layer was not found in *Aplodontia*.

*M. abductor hallucis*.—Well developed in the rodents examined. Arises from plantar surface of navicular and second cuneiform bones; inserts medially on plantar surface of proximal phalanx of hallux where is a large sesamoid bone.

*M. abductor ossis metatarsi quinti*.—In pocket gophers a stout ligament, running from plantar aspect of calcaneus to tuberosity of fifth metatarsal bone. In squirrels, *Aplodontia*, and wood rat it is muscular. In *Dipodomys* this muscle is partly fleshy, whereas in *Allactaga*, a jerboa (Howell, 1932), it has arrived at the ligamentous condition, apparently independently.

*M. abductor digiti quinti*.—In several specimens of *Thomomys* I was unable to find this muscle; in others and in *Geomys* it is present but slender. Arises from lateral surface of calcaneus, deep to preceding ligament; inserts on lateral side of first phalanx near base. In *Aplodontia* and in squirrels it is hardly separable from abductor ossis metatarsi quinti, but otherwise similar. This muscle and the preceding one were probably derived from a single muscle in the premammalia (cf. McMurrich, 1907).

*Mm. lumbricales*.—In pocket gophers, only slips to medial sides of fourth and fifth digits distinct; latter much the larger. There are three large muscles in *Citellus*, four in *Aplodontia*. They insert on the three or four lateral digits. They arise from the tendon of flexor fibularis.

*Mm. adductores*.—Apparently absent in pocket gophers, but in *Citellus* and in *Aplodontia* there are two. Adductor hallucis inserts on lateral side of hallux; adductor digiti quinti on medial side of fifth digit; both insert on the proximal phalanges. They arise from ligaments superficial to the tendon of peroneus longus and from the plantar surface of the third cuneiform.

*M. flexor hallucis brevis*.—Appears to represent the deep part of flexor hallucis brevis in man. In pocket gophers arises from plantar surface of third cuneiform; from base of first metatarsal in *Citellus* and *Aplodontia*. Inserts on sesamoid bones at metatarsophalangeal joints. From relationships and insertion it is probably one of the interossei rather than, as McMurrich (1907) concluded, a derivation from one of the lumbricales.

*Mm. interossei*.—Two to each of the four lateral digits. In pocket gophers, muscles to second digit arise from the third cuneiform and the base of the second metatarsal; the other muscles arise from the cuboid and from the bases of respective metatarsal bones. Insert on sesamoid bones at metatarsophalangeal joints. In *Citellus* and *Aplodontia*, the medial interosseous muscle of the second digit and those of the third arise from the third cuneiform, whereas the interossei of the fourth and fifth digits take origin from the cuboid. Fibers also arise from the bases of the respective metatarsal bones, as in pocket gophers; insertions are similar to those in the latter animals.

## NERVOUS SYSTEM

The nervous system was investigated in six specimens of *Thomomys*, four of which were of the species *bottae*, two of *bulbivorus*.

The brain has been described by Herrick (1892) in *Geomys*; that of *Thomomys* is similar.

### SPINAL MEDULLA

The spinal medulla, or cord, lies in the vertebral canal and extends as far caudad as the middle of the sacrum. Thirty-five spinal nerves arise from the cord: eight cervicals, twelve (or thirteen) thoracics, seven (or six) lumbar,

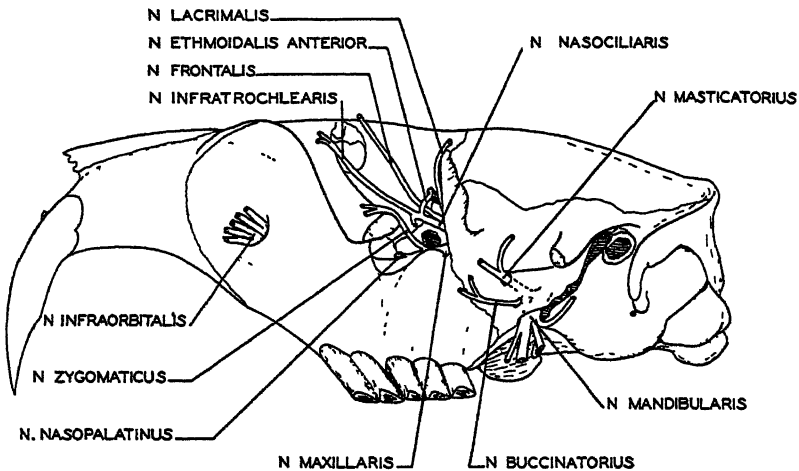


Fig. 22. Branches of trigeminal nerve, in relation to skull (*Thomomys bottae*),  $\times 2$ .

five sacrals, and usually three caudals. The spinal cord differs scarcely at all from this structure as described in the cat (Reighard and Jennings, 1930).

### CRANIAL NERVES

The first four cranial nerves do not differ in their relations and courses from these nerves as described in the cat (Reighard and Jennings, 1930).

*N. trigeminus* (V).—Agrees in roots, ganglion, and main branches with the nerve as described in other mammals.

(1) *N. ophthalmicus* (fig. 22). First branch of trigeminal passes out from cranial cavity through dorsal angle of sphenorbital fissure, dividing into lacrimal, frontal, and nasociliary nerves. Lacrimal nerve runs dorsad to dorsocaudal angle of orbit; branches to supply skin of this region. Frontal nerve runs dorsocranial on medial surface of orbit, supplying skin between orbits and suborbital vibrissae. Supratrochlear nerve appears to be absent. Nasociliary nerve supplies branches to eyeball and ciliary ganglion; gives off anterior ethmoid branch. This enters cranium by foramen (usually confluent with sphenorbital fissure); passes through cribriform plate of ethmoid; ends in nasal cavity. Rest of nasociliary continues as infratrochlear nerve, supplying skin anteromedial to eye.

(2) *N. maxillaris* (fig. 22). Arises from semilunar ganglion of trigeminal; passes almost immediately into open sphenopterygoid canal. Passes into orbit through sphenorbital fissure. While still in canal, gives off greater palatine branch to palate. In orbit, sphenopala-

tine nerve separates from maxillary; enters nasal cavity through sphenopalatine foramen. Maxillary then gives off zygomatic nerve which runs to anterolateral angle of zygoma; supplies skin in that region. Maxillary nerve, at this point known as infraorbital, enters infraorbital canal; gives branches to root of large upper incisor tooth; continues forward to emerge through infraorbital foramen. Infraorbital nerve supplies mystacial vibrissae and skin of rostrum.

(3) *N. mandibularis* (fig. 22). Runs ventrad from origin, the semilunar ganglion, emerging from cranium through foramen ovale. Five branches are given off almost immediately.

1. Medial branch supplies internal pterygoid muscle.

2. Masticatory nerve enters alisphenoid canal with internal maxillary artery. Here it usually gives off buccinator nerve which passes out of canal by separate foramen (see fig. 22). In some specimens of *Thomomys bottae* (and regularly in *T. talpivorus*) it does not divide until it passes out into infratemporal fossa. Anterior temporal nerve, which supplies orbital part of temporal muscle, arises from buccinator. Rest of buccinator passes to cheek where it branches. The masticatory nerve branches to temporal muscle; passes through mandibular notch; pierces posterior part of masseter medialis (see fig. 11, right), which it supplies; then runs between masseter lateralis and anterior part of masseter medialis, supplying both. Large branch pierces anterior part of masseter lateralis profundus; supplies superficial masseter muscle. Masticatory nerve ends by branching into anterior part of masseter lateralis profundus in front of orbit.

3. Large lingual nerve passes to tongue. It is joined by chorda tympani as usual.

4. Auriculotemporal nerve runs laterad on surface of external pterygoid muscle to posterior margin of jaw. Turns dorsad; passes deep to anterior branch of facial, sending branch to join that nerve. Supplies skin in front of ear, and genal vibrissae.

5. Inferior alveolar nerve is main continuation of mandibular nerve. Mylohyoid nerve separates from inferior alveolar on surface of external pterygoid muscle; passes to mylohyoid group of muscles. Inferior alveolar nerve supplies roots of lower teeth; emerges through mental foramen as mental nerve; supplies skin of chin region and submental vibrissae.

*N. abducens* (VI).—Does not exhibit any peculiarities in pocket gophers.

*N. facialis* (VII).—Arises from medulla oblongata and enters the internal auditory meatus. Emerges from petrotympanic bone through stylomastoid foramen. Divides into three branches: Nerve to stylohyoid and posterior belly of digastric, preauricular, and postauricular nerves. This last runs dorsad; supplies postauricularis muscle, occipitalis, sphincter colli primitivus, and anterior part of retractor of pouch. Preauricular nerve divides into a number of branches. Most ventral one supplies fibers to parotid gland, superficial sphincter muscle, and sterno-auricularis. Marginal mandibular branch runs along ventral margin of masseter superficialis; supplies orbicularis oris and associated muscles. Buccal branch runs across belly of masseter to rostrum; supplies buccinator muscle and facial muscles of that region, anastomosing with zygomatic branch. This runs along dorsal border of masseter muscle; supplies branches to facial muscles of that region. Temporal branch accompanies supraorbital artery and vein over dorsocaudal margin of orbit, supplying Mm. preauricularis, auriculolabialis, and orbicularis oculi. Chorda tympani is small; not distinctive.

*N. acousticus* (VIII).—Not dissected in the pocket gopher.

*N. glossopharyngeus* (IX).—Emerges from cranium by jugular foramen with vagus and accessory nerves. Supplies slender stylopharyngeus muscle; passes between this muscle and stylohyoideus into tongue. Branches supply pharynx and posterior part of tongue.

*N. vagus* (X).—Leaves cranial cavity by jugular foramen. As it emerges from the foramen, gives off branches to sympathetic system and superior laryngeal nerve to larynx. Runs parallel with internal jugular and common carotid, between these as far caudad as aortic arch on left side and subclavian artery on right side. Here recurrent laryngeal nerves given off. These pass around arch of aorta or subclavian, as case may be; run cranial in groove between esophagus and trachea. They branch to esophagus and to larynx.

Cervical cardiac branch single on each side. It separates from vagus nerve opposite first rib; passes to heart. Thoracic cardiac branches on right side come off from vagus opposite base of innominate artery; on left side arise caudal to dorsal aorta. These branches pass to heart also.

Vagus gives off branches to trachea and to pulmonary plexus. Small twigs also pass to esophagus. Left vagus nerve becomes ventral near diaphragm. Right vagus supplies dorsal surface and greater curvature of stomach; left vagus supplies lesser curvature and ventral surface. Branches caudal to stomach not followed.

*N. accessorius* (XI).—Arises by several roots from medulla oblongata with vagus, and by a number of roots from spinal medulla in series with these, between dorsal and ventral roots of spinal nerves. It is probably a division of the vagus; its nuclei probably represent an extension of the nucleus ambiguus. Emerges from cranium through jugular foramen.

Passes to deep surface of sternomastoid muscle, which it supplies. Branches arise from second and third cervical nerves which unite and then redivide into four twigs; these unite with branches of accessory, and accessory itself. A few millimeters caudal to this anastomosis, accessory nerve gives off branch to clavicular fibers of trapezius; passes to deep surface of that muscle. Accessory runs obliquely to spine of scapula near base of acromion, then runs parallel with spine in dorsal direction as far as crest. In its course several branches supplied to trapezius muscle. Accessory nerve passes dorsal to crest, to deep surface of spinotrapezius, which it supplies. Becomes buried in belly of spinotrapezius, taking tortuous course to allow for contraction and relaxation of the muscle. Reaching caudoventral border of spinotrapezius, it crosses intervening fascia and enters retractor muscle of pouch where it terminates.

*N. hypoglossus* (XII).—Arises from ventrolateral surface of medulla oblongata by several roots which pass out from cranial cavity by several (two or three) hypoglossal foramina. It crosses ventrally over vagus and sympathetic nerves, internal and external carotid arteries, and internal jugular vein. Then passes lateral to styloglossus and hyoglossus muscles, to which it gives branches; runs between geniohyoid and genioglossal muscles; enters tongue. Supplies intrinsic muscles of tongue, geniohyoideus and genioglossus. No anastomosis with cervical nerves; infrahyoid group supplied entirely by first and second cervicals.

## SPINAL NERVES

### *Dorsal rami*

Dorsal rami divided into two branches: medial and lateral. In pocket gophers first cervical nerve appears to lack a dorsal cutaneous branch. Dorsal cutaneous branches of second, third, and fourth unite to form greater occipital nerve. This pierces *M. splenius* near middle; supplies skin of occipital region. Cutaneous branches of fifth to eighth cervical nerves and first four thoracic emerge from dorsal muscle mass near middorsal line; they are medial branches. Caudal to this, dorsal cutaneous nerves are lateral branches. Last dorsal cutaneous nerve found is a branch of second sacral nerve. Lumbar and more caudal thoracic cutaneous nerves directed obliquely caudad; first lumbar, for example, supplies skin over crest of ilium. All pursue long, tortuous courses; some caudal thoracic cutaneous nerves are 35 mm. in length.

Lateral branches of first thirteen dorsal rami supply epaxial muscles of back; medial branches of more caudal nerves have this function. But particular muscles innervated by these branches were not determined by me.

### *Ventral rami*

Ventral rami complicated, except in thoracic region, by formation of plexus for limbs. The intercostal nerves remain relatively primitive. Run in intercostal spaces behind each rib; supply intercostal and related muscles, such as serratus posterior and transversalis thoracis. Lateral cutaneous branches given off from these nerves; emerge near insertion of serratus posterior; divide into two branches supplying skin. On skin numerous branches and anastomoses can be seen. Medial terminal branches of intercostal nerves pierce *Mm. rectus abdominis* and *pectorales*; supply *rectus abdominis* before piercing it; end in skin near mid-

The more caudal intercostal nerves run for parts of their courses between transverse and internal oblique muscles of the abdomen. The iliohypogastric nerves have similar courses to the intercostals; they will be described with the lumbosacral plexus.

**Cervical plexus (fig. 23).** Hardly separate from the brachial. Formed by ventral rami of first three cervical nerves and part of the fourth. Small ventral ramus of first cervical nerve

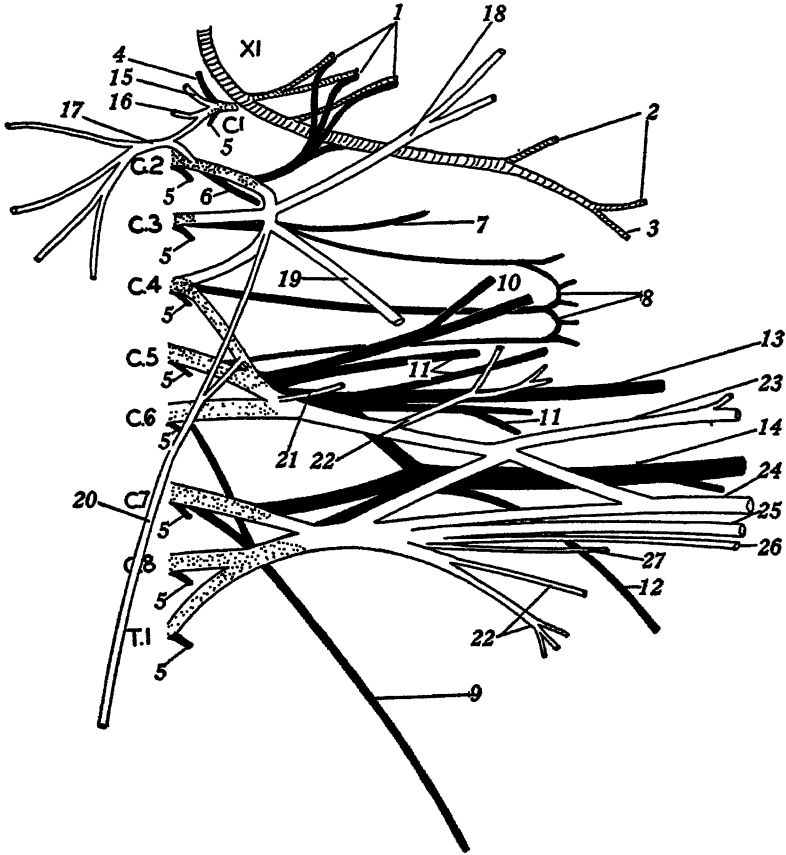


Fig. 23. Cervicobrachial plexus. [Black, dorsal branches; white, ventral branches.] XI, N. accessorius; C.1 to C.8, ventral rami of cervical nerves; T.1, ventral ramus of first thoracic nerve; 1, N. to sternocleidomastoideus; 2, N. to trapezius; 3, N. to retractor of pouch; 4, N. to rectus capitis lateralis; 5, N. to scalenus; 6, N. to omocervicalis; 7, N. to occipitoscapularis; 8, Nn. dorsales scapulae; 9, N. thoracalis longus; 10, N. suprascapularis; 11, Nn. subscapulares; 12, N. thoracodorsalis; 13, N. axillaris; 14, N. radialis; 15, N. to rectus capitis anterior; 16, N. to longus capitis; 17, infrahyoid trunk; 18, N. cervicalis ascendens; 19, N. cervicalis descendens; 20, N. phrenicus; 21, N. subclavius; 22, Nn. thoracales anteriores; 23, N. musculocutaneus; 24, N. medianus; 25, N. ulnaris; 26, N. cutaneus antibrachii medialis; 27, N. cutaneus brachii medialis.

emerges through atlantal foramen in atlas. Second cervical nerve larger; emerges from vertebral canal through groove in atlas, dorsal to caudal articular surface. Other nerves pass out from vertebral canal by way of intervertebral foramina. Plexus consists of intercommunications between the four nerves. Medial communicating branches of first two nerves unite to form a trunk to the infrahyoid muscles. Second, third, and fourth cervical nerves unite to form an *m*-shaped complex. Part of fourth nerve enters upper trunk of brachial plexus.

Two cutaneous branches:

(1) Ascending cervical nerve arises from loop between second and third nerves; runs deep to sternocleidomastoid complex; emerges between this and *M. trapezius*; supplies skin of region behind ear and of neck.

(2) Descending cervical nerve is apparently a continuation of the third nerve, but it probably contains fibers from the second and fourth also. Runs caudad underneath sternocleidomastoid muscle; emerges between insertions of cleido-occipitalis and trapezius. Divides into five branches (supraclavicular nerves) which supply skin of shoulder region.

Muscular branches of plexus are dorsal (lateral) and ventral (medial). Dorsal branches usually lie deep to scalenus complex.

(1) A branch arises from first cervical nerve; supplies *M. rectus capitis lateralis*.

(2) Branches from second, third, and fourth nerves supply adjacent parts of *M. scalenus*.

(3) A branch leaves second cervical near intervertebral foramen; passes to deep surface of *M. omocervicalis* which it supplies.

(4) Two of three dorsal scapular nerves arise from third and fourth cervicals. These will be described with the dorsal scapular nerve of the fifth cervical.

(5) Second and third cervical nerves communicate with accessory nerve. Several branches of this communicating nerve pass to sternomastoid, cleidomastoid, cleido-occipitalis, and trapezius muscles, in association with branches of accessory nerve to these.

Ventral, or medial, branches of cervical plexus run mediad.

(1) A small branch arises from first cervical; supplies *M. rectus capitis anterior*.

(2) Short branches from the four cervical nerves supply *Mm. longus colli* and *longus capitis*.

(3) *Infrahyoid trunk* (see fig. 23, 17), arising from loop between first and second cervical nerves, runs obliquely caudomediad on surface of *longus colli*. Gives off slender branch to thyrohyoid muscle opposite root of second cervical nerve. Some little distance caudad, nerves to sternothyroid and sternohyoid pass from trunk to these muscles; rest of trunk runs caudad and laterad as nerve to omohyoid. In pocket gophers there is no *descendens hypoglossi*.

**Brachial plexus** (fig. 23). Ventral rami of fifth and sixth cervical nerves, with part of the fourth, unite to form upper (cranial) trunk. Seventh cervical alone forms middle trunk. Lower (caudal) trunk is composed of the united eighth cervical and first thoracic nerves; these are separate in some specimens, however. The divisions of the plexus are similar to those in man; what appear to represent lateral and medial cords are formed, but the posterior cord is not distinct, its branches being widely separated. The lateral cord receives contributions from three trunks, the medial cord only from the more caudal two.

Dorsal (posterior) branches of the brachial plexus probably correspond to lateral branches of intercostal nerves.

(1) Small branches arise from each of the cervical nerves, supplying cervical part of scalenus complex.

(2) *Nn. dorsales scapulae* (fig. 23, 8). Dorsal branches of third, fourth, and fifth cervical nerves arise near intervertebral foramina. Most cranial of these runs along cranial margin of *M. levator scapulae*; divides about one-third the way along that muscle. The larger branch passes to deep surface of *M. occipitoscapularis* which it supplies; the smaller continues along levator scapulae, giving off twigs to this. At vertebral border of scapula it communicates with middle dorsal scapular nerve. Second or middle nerve runs between first and second slips of levator scapulae. It branches to that muscle; near the insertion communicates with other two dorsal scapular nerves. Branches, which supply rhomboideus, arise from both of these loops. Third dorsal scapular nerve similar to second, runs between second and third slips of levator scapulae, which it supplies. Ends in communicating branch mentioned above.

(3) *N. thoracalis longus*. Arises by union of dorsal branches from sixth and seventh cervical nerves, in series with dorsal scapulars. Runs on lateral surface of *M. serratus anterior* supplying this and caudal part of levator scapulae. Roots of this nerve, like dorsal scapular nerves, lie deep to *M. scalenus*.

(4) *N. suprascapularis*. Most cephalic branch of brachial plexus ventral to scalenus. Arises from upper trunk of plexus; runs in transverse direction to suprascapular notch. Passes to lateral surface of scapula, deep to muscles covering that surface; supplies supra- and infraspinatus muscles.

(5) *Nn. subscapulares*. Three in pocket gophers. First two arise from dorsal side of upper trunk of plexus. Third subscapular nerve arises from middle trunk; accompanies axillary nerve for some distance. Supply Mm. subscapularis and teres major.

(6) *N. thoracodorsalis*. In series with subscapulars. Arises from dorsal division of lower trunk of brachial plexus, associated with radial nerve. Supplies M. latissimus dorsi.

(7) *N. axillaris*. Arises from dorsal divisions of upper and middle trunks, although contribution of upper trunk is small. Axillary nerve passes, along with posterior humeral circumflex artery and vein, through quadrilateral space bounded by M. teres major, scapula, long head of M. triceps, and shoulder joint. Supplies Mm. deltoideus and teres minor, and skin of lateral side of upper arm.

(8) *N. radialis*. Formed by union of dorsal divisions of middle and lower trunks, with some contribution from upper trunk. Largest branch of brachial plexus. Radial nerve crosses axilla; passes to lateral surface of humerus, running in spiral manner around that bone between long and medial heads of triceps, between lateral head of triceps and brachialis. As it passes caudal margin of latissimus tendon, gives off large branch to supply long head of triceps and dorsoepitrochlearis. Another branch separates from radial nerve; supplies lateral and medial heads of triceps, anconeus, and part of brachialis. Radial nerve emerges on cranial surface of arm between triceps and brachialis; here divides into deep and superficial radial nerves. The absence of M. brachioradialis appears to permit the cutaneous branches of the radial nerve to unite; the superficial ramus supplies the skin of the dorsal sides of both forearm and hand.

Ramus profundus passes deep to Mm. extensores carpi radiales, supplying these. Opposite lateral epicondyle a small branch supplies M. supinator from the deep surface. Deep ramus then passes between M. supinator and head of radius. In the forearm branches supply Mm. extensor digitorum longus, extensor digiti quinti proprius, abductor pollicis longus, extensor indicis et pollicis, and extensor carpi ulnaris. Ramus profundus appears to end near the middle of the forearm, but it is possible that the carpal articular branch was overlooked.

Ventral branches of the brachial plexus supply the flexor muscles of forelimb and shoulder.

(1) Small branches arise from roots of all nerves of the plexus; supply M. longus colli.

(2) *N. phrenicus* (fig. 23, 20). Arises by two or three roots: one, a medial branch of third cervical; another from fourth cervical near union of this nerve with upper trunk of brachial plexus. In some specimens a third root arises from fifth cervical nerve. Runs caudad and slightly mediad; supplies muscle of diaphragm.

(3) *N. subclavius*. Arises from ventral division of upper trunk, before this unites with similar division of middle trunk to form lateral cord of plexus. Otherwise similar in its relationships to anterior thoracic nerves. Supplies M. subclavius.

(4) *Nn. thoracales anteriores*. Two in number; but medial nerve may divide soon after its origin. Lateral anterior thoracic nerve arises from lateral cord, but in some specimens it receives fibers from the three trunks of the brachial plexus. Medial anterior thoracic nerve arises from medial cord; receives fibers from middle and lower trunks. Supply pectoral group of muscles.

(5) *N. musculocutaneus*. Arises from lateral cord of plexus. Near the shoulder joint a branch supplies short part of coracobrachialis. Musculocutaneous nerve passes between two parts of M. coracobrachialis, supplying long part; supplies short head of M. biceps; runs between biceps and brachialis; near middle of upper arm it sends branches to latter muscle and to long head of biceps. Continues as lateral cutaneous nerve of forearm; emerges between long head of biceps and brachialis near elbow; runs in superficial fascia of forearm, supplying skin of lateral surface. Some fibers anastomose with the superficial radial nerve, and the musculocutaneous nerve may communicate with the median near the elbow.



(6) *N. medianus*. Arises by two heads, as is usual in mammals: one from lateral cord, other from median, both short. Runs with ulnar and medial cutaneous nerves to elbow. In elbow passes between biceps and pronator teres. Opposite elbow joint, branches supply those flexor muscles which arise from medial epicondyle. Large branch of median, volar interosseous nerve, passes deep to these muscles; supplies radial and condylar heads of flexor digitorum sublimis and flexor pollicis longus; then runs deep to flexor carpi radialis, between it and radial head of flexor profundus. In wrist, branches supply skin of radial side.

Median nerve enters manus; supplies abductor pollicis brevis and skin of radial half of volar surface. The volar fascia is dense, and the various branches of the median nerve in the manus were not followed satisfactorily.

(7) *N. ulnaris*. Arises from medial cord; runs with median nerve and medial cutaneous nerve across axilla and down arm to elbow. Ulnar nerve then passes between medial head of *M. triceps* and *M. epitrochleo-aneoneus*, supplying latter by a slender branch. Deep to epitrochleo-aneoneus a branch supplies flexor carpi ulnaris; a little farther distad a branch is given off to ulnar head of flexor digitorum profundus. Ulnar nerve then continues distad between these two muscles. Near middle of forearm it gives off dorsal ramus of hand, which supplies skin on ulnar side of dorsum of manus. Volar cutaneous branch supplies skin of wrist on volar and ulnar sides. In the manus the branches were not satisfactorily dissectable because of dense fascia.

(8) *N. cutaneus antibrachii medialis*. Arises from medial cord of plexus; runs with median and ulnar nerves to elbow; passes to superficial fascia of forearm, supplying skin superficial to *M. flexor carpi ulnaris* and adjacent thereto.

(9) *N. cutaneus brachii medialis*. Minute in pocket gophers. Arises from medial cord; supplies skin on proximal medial surface of arm.

**Lumbosacral plexus**, including pudendal plexus (figs. 20, 24). Formed by second to seventh lumbar nerves and first three or four sacrals. In some specimens the second lumbar did not contribute. Ventral rami of lumbar nerves form longitudinal trunk which receives contributions from first three sacral nerves. Sacral nerves united by irregular loops. Roots of plexus short; longitudinal trunk lies in groove formed by ventrally curved transverse processes of lumbar vertebrae.

The branches of the lumbosacral plexus, with the exception of the first two, the iliohypogastric nerves, and the last, the hemorrhoidal, are classifiable into dorsal and ventral nerves.

*Nn. iliohypogastrici* (fig. 24, 1).—Two in pocket gophers. One arises from longitudinal trunk opposite caudal end of third lumbar vertebra, or from second lumbar nerve, when that is independent. The other nerve separates from common longitudinal trunk opposite fourth lumbar vertebra. After giving off lateral cutaneous branches, they pass through body wall cranial to inguinal ligament, in company with ilio-lumbar artery and vein. Supply skin of inguinal region.

Dorsal branches of lumbosacral plexus do not differ from ventral ones except in distribution; they supply extensor muscles and skin of the primitively dorsal surface.

(1) *N. femoralis*. Arises from longitudinal trunk opposite sixth lumbar vertebra; passes between *M. psoas major* and *M. iliacus*, supplying these; enters thigh on ventral surface of *M. iliacus* (fig. 21). Pectineal branch separates opposite lesser trochanter; supplies part of pectineus muscle. Femoral nerve passes to medial surface of rectus femoris; here gives off a trunk which passes between rectus femoris and the vasti, supplying these muscles. Another branch arises near knee to supply distal part of vastus medialis; slightly more distad, twig given off to knee joint. Femoral nerve, now known as saphenous, accompanies great saphenous vessels along medial surface of leg, supplying skin of that region.

(2) *N. peroneus communis*. Almost completely distinct from the tibial nerve which accompanies it in the thigh. Separates from ventral elements of longitudinal trunk before these unite with the branch from sacral nerves. Arises from plexus opposite second sacral vertebra. In pelvis it gives off two branches. Superior gluteal nerve arises first; it gives off branches to *Mm. piriformis*, *gluteus medius*, *gluteus minimus*, and *tensor fasciae latae*. Inferior gluteal nerve arises close to superior nerve; two branches supply *M. gluteus maximus*, one supplies *M. femorococcygeus*.

Common peroneal nerve passes through greater sciatic foramen; continues distad in same connective tissue sheath with tibial nerve, but separable with little difficulty. Near level of gluteal tuberosity, lateral sural nerve arises; passes between *M. femorococcygens* and *M. biceps femoris*; supplies skin of lateral surface of leg and of lower thigh. Branch of common peroneal nerve supplies knee joint; another, peroneal anastomotic branch, unites with sural nerve on belly of gastrocnemius.

In the leg, common peroneal nerve divides into deep and superficial rami. Superficial peroneal nerve supplies *M. peroneus brevis* and crural parts of *M. extensor digitorum brevis*; passes deep to *peroneus longus*; runs between that and *extensor digitorum longus*, emerging near lower third of leg; accompanies tendon of long extensor to dorsal surface of foot, supplying skin of its lateral moiety.

Deep peroneal nerve separates from superficial ramus as both pass under *peroneus longus*. Deep ramus supplies this muscle, *extensor digitorum longus*, *tibialis anterior*, and *extensor hallucis longus*. Deep peroneal nerve runs beneath *extensor digitorum longus* to ankle; a branch supplies ankle joint; another supplies pedal parts of *extensor brevis*. Deep peroneal nerve ends in skin on mediodorsal surface of foot.

Ventral branches of the lumbosacral plexus supply muscles and skin of the primitively ventral part of the limb which, because of rotation, is now chiefly caudal and medial.

(1) Twigs from lumbar nerves supply *Mm. quadratus lumborum* and *psoas minor*.

(2) *N. genitofemoralis*. Apparently includes also the inguinal part of ilioinguinal nerve, judging from its distribution. Arises from common longitudinal trunk opposite caudal end of fourth lumbar vertebra; runs caudad on medial side of *psoas* muscles. Opposite first sacral vertebra passes ventrally over tendon of *psoas minor* and femoral vessels. Here a branch (fig. 24, 4) accompanies femoral vessels to body wall; enters abdominal muscles, supplying these; terminates in *rectus abdominis*. This branch seems to correspond to the inguinal nerve, but there is no cutaneous branch.

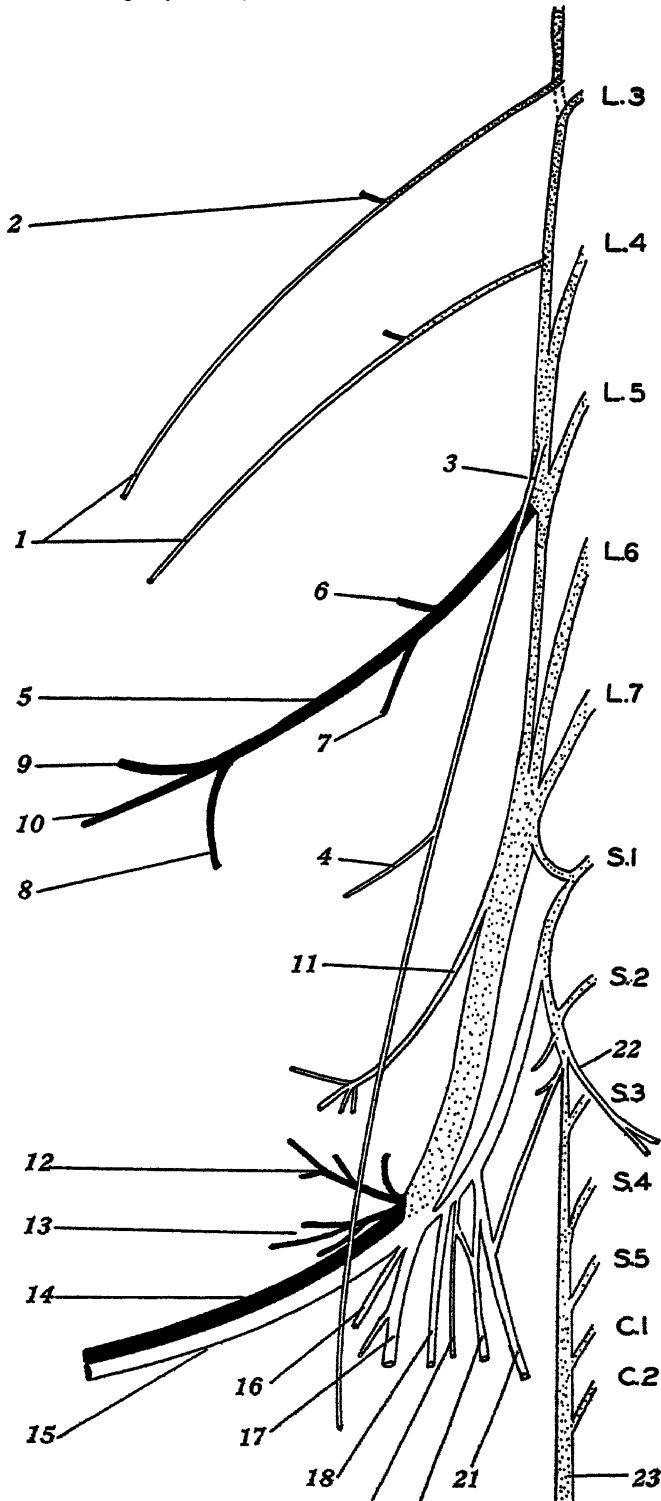
Rest of genitofemoral nerve runs caudad along ventral margin of pubis to symphysis, then divides; its branches supply scrotal or vulvar region and adjacent skin of leg.

(3) *N. obturatorius*. Arises from common trunk of lumbar plexus opposite first sacral vertebra; passes out of pelvis through obturator foramen. First branch runs mediad, between *Mm. adductores longus* and *brevis*, supplying these by small branches; emerges on medial surface of thigh; runs caudad to *M. gracilis*, in which it ends. Second branch passes deep to *M. adductor brevis*, between that and *adductores magnus* and *minimus*, supplying the three. Two small mediocaudal branches supply *M. obturator externus*. In pocket gophers the obturator nerve does not appear to have a cutaneous branch.

(4) *N. tibialis*. Arises from lumbosacral plexus opposite fourth sacral vertebra. Formed by union of longitudinal trunk from lumbar nerves with branch coming from loop between second and third sacral nerves. Gives off almost immediately two branches: one is the large "nerve to the hamstring muscles"; the other branch supplies *Mm. gemelli* and *quadratus femoris*.

Tibial nerve runs with common peroneal down the thigh, lying on *Mm. adductor magnus* and *caudofemoralis*. Near knee the two nerves separate. At this level, sural nerve arises; passes to lateral surface of gastrocnemius, where it is joined by peroneal anastomotic branch. Resulting nerve runs to lateral surface of ankle; divides into two branches: one supplies skin on lateral surface of foot; other passes mediad, to ankle joint and skin of plantar surface of foot.

Tibial nerve supplies *M. plantaris* and two heads of *M. gastrocnemius*; passes between *plantaris* and medial *gastrocnemius*. Here other branches supply *soleus*, *tibial* and *fibular flexors*, *tibialis posterior*, and *popliteus*. Tibial nerve runs between *plantaris* and *gastrocnemius* muscles almost to ankle; then passes to medial surface of leg; divides into lateral and medial plantar nerves. Latter supplies skin of medial half of sole and muscles of that region: *abductor hallucis*, *flexor hallucis brevis*, and *flexor digitorum brevis*. Lateral plantar nerve supplies skin of lateral side of sole and *Mm. abductor digiti quinti*, *lumbricales*, and *interossei*.



(5) *N. cutaneus femoris posterior*. Arises from sacral root of tibial nerve; lies between fat and nerve to obturator internus; passes between *M. femorococcygeus* and *M. biceps femoris*; supplies skin of laterocaudal surface of thigh.

(6) *N. cutaneus perforans*. Arises from union of two branches of sacral plexus, one associated with posterior cutaneous nerve, the other with the pudendal. Does not pierce sacrotuberous ligament in pocket gophers; emerges behind its caudal border. Supplies skin medial to area supplied by posterior cutaneous nerve.

(7) *N. pudendus*. Arises by two roots; one a branch from the loop between third and fourth sacral nerves, the other comes off from sacral root of tibial nerve. Pudendal nerve runs along dorsal border of ischium, then ventrad to perineal region. Supplies skin and muscles of this region; terminates as dorsal nerve of penis, or of clitoris, as case may be.

(8) Small branches from sacral nerves supply other caudal flexor muscles and the perineal group.

*N. hemorrhoidalis*.—Large visceral branch of sacral plexus arises at level of third sacral nerve. Runs mediad, branching to rectum and bladder.

### Nerves of the tail

Ventral rami of caudal nerves, usually three in number, unite together to form large longitudinal trunk (fig. 24, 23), continuous with last loop of sacral plexus, much as in the cat (Reighard and Jennings, 1930). This longitudinal nerve supplies muscles of tail and skin of its ventral surface. The end of the tail is well supplied with nerves; it is probably an important sense organ.

## DIGESTIVE AND RESPIRATORY SYSTEMS

### DIGESTIVE SYSTEM

*Oral cavity*.—In pocket gophers this does not correspond to that of most other mammals, since a secondary mouth opening is formed behind the incisor teeth by the fusion of the palatal lobes of the upper lip. The sides of the lower lip do not fuse, but are closely approximated. The secondary mouth opening is closed by the contraction of *M. buccinator* and by the large tongue; this prevents entrance of earth when the incisors are used in digging.

*Palate*.—Hard palate extends to level of third molar tooth. Palatal rugae, or ridges, present in anterior part of hard palate. Three large diastemal ridges, one near raphe of upper lip, other two near base of premolar tooth. First ridge V-shaped, with apex directed anteriorly; it is the highest. In *Thomomys* a pair of papillae on anterolateral surfaces of first ridge beside which vomeropalatine ducts open. In *Geomys*, ducts present, but papillae vestigial. Second ridge nearly straight, transversely placed, considerably smaller. Third ridge just anterior to root of premolar, still lower than others; it may be irregular. Rugae between cheek teeth poorly developed with exception of first; three, four, or five in number. More or less V-shaped with apex directed caudad. Two halves of ridges frequently remain separate. Two rugae situated between premolars, one runs between each pair of molars, but last one or two may be obsolete.

Soft palate, muscular and thick. Extends between medial pterygoid plates of each side, forming floor of nasopharynx. Caudal margin opposite occipitosphenoidal suture.

*Teeth*.—Figured and rather completely described by Merriam (1895). Deciduous premolar very similar to that of heteromyine forms; one of slightly worn molars figured by Merriam resembles description of molar teeth of *Entoptychus* of the Oligocene.

Fig. 24. Lumbosacral plexus. [Black, dorsal branches; white, ventral branches.] L.3 to L.7, ventral rami of lumbar nerves; S.1 to S.5, ventral rami of sacral nerves; C.1 and C.2, ventral rami of caudal nerves; 1, *Nn. iliohypogastrici*; 2, lateral branches of same; 3, *N. genitofemoralis*; 4, *N. inguinalis*; 5, *N. femoralis*; 6, *N. to iliacus*; 7, *N. to psoas major*; 8, *N. to pectineus*; 9, *N. to extensor quadriceps*; 10, *N. saphenus*; 11, *N. obturatorius*; 12, *N. gluteus superior*; 13, *N. gluteus inferior*; 14, *N. peroneus communis*; 15, *N. tibialis*; 16, *N. to quadratus femoris*; 17, *N. to hamstring muscles*; 18, *N. cutaneus femoris posterior*; 19, *N. to obturator internus*; 20, *N. cutaneus perforans*; 21, *N. pudendus*; 22, *N. hemorrhoidalis*; 23, longitudinal caudal trunk.

**Salivary glands.**—Parotid gland large and irregular, number of lobes loosely connected together, filling space between lower jaw and shoulder. Parotid duct arises near angle of jaw; runs anteriorly across superficial masseter muscle; pierces buccinator muscle near posterior boundary; opens into oral cavity near base of upper premolar tooth. Submaxillary gland lies ventromedial to parotid; smaller, more compact, otherwise quite similar to parotid. Submaxillary duct runs anteriorly, passing between anterior belly of digastric and angle of jaw. Opens in groove between tongue and jaw about level of lower third molar. Small sublingual gland lies along submaxillary duct near opening; its separate duct opens near submaxillary duct.

**Tongue.**—Large, fleshy. Anterior three-fourths with small, slightly recurved filiform papillae. Single vallate papilla situated in midline near base. Tuckerman (1890) found fungiform papillae in pocket gophers, but these are not distinguishable under the dissecting microscope. Tongue free for anterior third; besides its use during mastication, it serves to close secondary mouth opening.

**Pharynx and esophagus.**—Auditory tube vestigial; I was unable to find its opening into pharynx. Esophagus narrow, almost straight.

**Stomach** (fig. 25).—Simple, roomy. Greater curvature somewhat more than half circle. Long axis, almost transverse to axis of body, some 32 mm. in *Thomomys bulbivorus*, slightly less in specimens of *bottae*. Greatest depth, lesser to greater curvatures, approximately 20 mm. Size varies noticeably according to amount of food contained in stomach. Cardiac end in contact with left body wall; pyloric constriction slightly to right of median line. Lesser curvature considerably shorter than greater; V-shaped, apex of V divides stomach into two regions; blind cardiac sac to left, pyloric part to right. Esophagus empties immediately to the left of the middle. Pylorus narrow, muscular; sphincter bands large. Small dorsal pocket usually formed by folds in this region.

Esophageo-gastric valve consists of a number of pointed flaps of different sizes arranged around opening of esophagus into stomach. Opposite openings of esophagus and pylorus, on greater curvature, is a large, thickened fundic gland. Mucosa of stomach here several times thicker than elsewhere; some openings of gland visible to naked eye. Sides of pyloric part of stomach also glandular, to lesser degree than fundus. No cornified layer in cardiac sac, such as in muroid rodents.

Both greater and lesser omenta small; former does not cover intestines as in the rat and in many other mammals. Greater omentum contains spleen and part of pancreas; it is fused to mesocolon as usual.

**Duodenum** (fig. 25).—Larger in diameter than rest of intestine with exception of caecum. Somewhat C-shaped; may be divided into four parts. The superior part (cf. Bonfert, 1928) between the pylorus and the entrance of the bile duct is, in *Thomomys bottae*, approximately 14 mm. long and 10 mm. wide at place of greatest diameter, near pyloric constriction. Directed to right and caudad. Common bile duct enters obliquely on ventral side of duodenum; opens into lumen of intestine at end of small, simple papilla.

Descending part of duodenum runs nearly caudad; some 28 mm. long in *Thomomys bottae*. Diameter gradually decreases to 6 mm. Opposite last lumbar vertebra, descending duodenum turns to left and passes into transverse part, hardly separable from descending duodenum or from ascending part. Latter runs cranial; then turns ventrad and passes into jejunum-ileum. Transverse and ascending parts together, some 25 mm. long in *Thomomys bottae*.

Duodenum suspended from dorsal body wall by part of dorsal mesentery, mesoduodenum. A secondary ligament, ligamentum caevoduodenale, connects ascending duodenum to mesocolon. Although the mesentery would appear to permit some movement of duodenum, latter is, in all specimens examined, in right side of abdominal cavity and lies along dorsolateral body wall.

**Jejunum-ileum.**—Rest of small intestine forms number of irregular folds on periphery of mesentery. Loops of small intestine not constant, of no important significance (cf. Mitchell, 1905, 1916). Length of this part of digestive tract varies in individuals and it is difficult to be sure it does not lengthen in death. In *Thomomys bottae*, measured by means of a thread

along middle, *in situ* and without stretching, it was from 245 to 300 mm. Slightly longer in *Thomomys bulbivorus*; in *Geomys bursarius* from 315 to 375 mm. Diameter gradually decreases from collapsed width of 6 mm. to one of 3.5 mm. near caecum.

**Caecum** (fig. 25).—Large, sacculated. Lies in dextral spiral, viewed from ventral side. First and largest sacculatation, ampulla coli, lies between entrance of ileum and colon proper. Two or three unequal sacculatations, diameter somewhat less than that of ampulla, form "body." J-shaped "tail," perhaps corresponds to the "vermiform appendix" of rabbit. In *Geomys*, ampulla coli smaller; body larger, with an additional sacculatation.

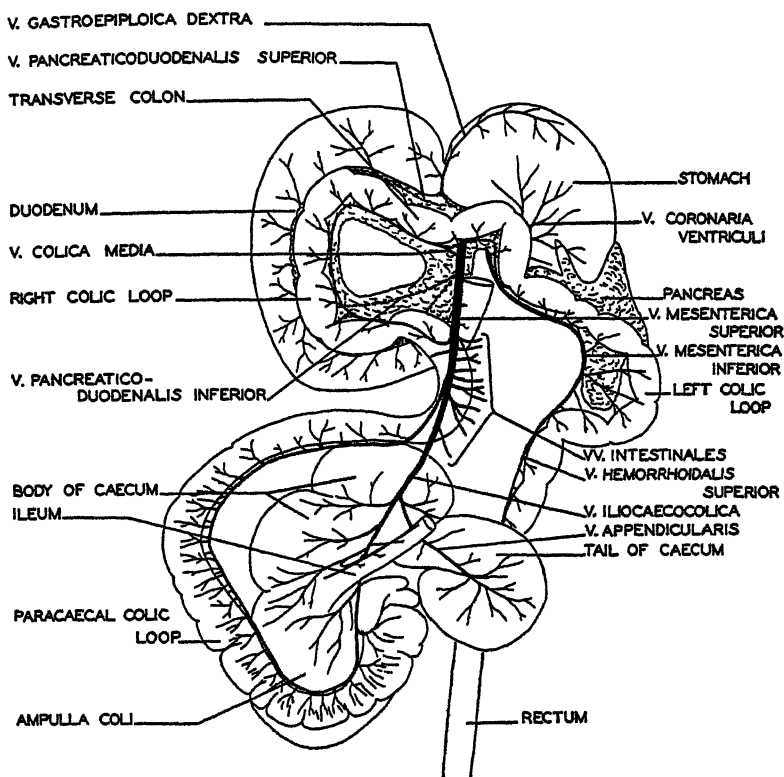


Fig. 25. Digestive system and portal vein (*Thomomys bottae*),  $\times 1$ . Stomach and intestines arranged, viewed from ventral side.

Ileum enters ampulla coli from dorsal side; opens in semicircular slit near valve between ampulla and body of caecum. Ileocaecal valve consists of puckered ridge on each side of opening, and a sphincter muscle. No flaps involved.

Valve separating ampulla coli and body of caecum consists of two large, loose flaps of intestinal wall, from dorsal and ventral sides of caecum. Two folds meet on lesser curvature, but are separate at greater curvature. Each external constriction extends into lumen of caecum as a valve. First comes from ventral side and lesser curvature of caecum; its free end reaches almost to dorsal wall. A little distad, toward tail of caecum, there is a fold from dorsal side and greater curvature. These two flaps together divide body of caecum into two compartments.

Between tail and body two more flaps, one dorsal and one ventral; these overlap considerably unless caecum distended. Still another pair of flaps extend inward, one from fold in lesser curvature of tail, the other from point nearly opposite. These two do not completely divide lumen of tail.

Caecum in *Geomys bursarius* more specialized than in *Thomomys*. Body divided into three compartments instead of two; separation more complete. Folds do not act together; extend almost to opposite wall; fused to wall except for narrow flap, so opening between compartments reduced to about a quarter of lumen of caecum at this place. Fold from lesser curvature between tail and body similar; other flap from dorsal side absent. Only one large valve in tail of caecum.

Valve between ampulla coli and paracaecal loop of colon consists of dorsal semicircular fold and small ventral flap, two together closing the opening. Also there seems to be a sphincter muscle.

*Colon* (fig. 25).—Consists of typical three parts; the ascending, transverse, and descending parts. First and part of second suspended on same mesentery as small intestine. Rest of colon suspended on mesocolon.

Ascending colon consists of two loops: paracaecal and right colic. Paracaecal loop (Tullberg, 1899) irregularly sacculated for most of length, particularly near beginning. Paracaecal loop runs along greater curvature of ampulla and body of caecum, united to them by mesentery. Several longitudinal muscle bands present at caecal end; these become reduced to single thick band on lesser curvature of loop and disappear near its distal end. In *Thomomys bottae*, colon near ampulla coli 15 mm. wide; reduced to diameter of 6 mm. after first third of paracaecal loop.

Paracaecal loop ends near middorsal line. Colon runs in cranial direction for some 35 mm., crossing duodenum ventrally; enters right colic loop. This follows transverse, descending, and superior parts of duodenum closely, its mesentery fused to mesoduodenum. Fecal pellets of typical elliptical shape (cf. Seton, 1909) formed at beginning of right colic loop. Here pellets are larger, softer than farther along colon; water content is reduced during passage.

Near pylorus, colon turns to left as transverse part. Lies dorsal to stomach; attached to greater omentum. In some specimens transverse colon nearly straight, in others with a shallow flexure.

Descending colon forms left colic loop which projects ventrally beside "tail" of caecum. In *Thomomys* this loop is small, but in *Geomys* large and usually double. Descending colon caudal to loop, or loops, runs to middorsal line; continues into rectum.

*Rectum*.—Short; runs nearly straight in pelvis to anal opening.

In *Thomomys bottae* the small intestine is nearly the same length as the large intestine; sometimes shorter, sometimes longer. Proportions in three specimens are respectively: 318 to 295; 342 to 288; and 337 to 374 mm. In *Geomys* the small intestine is considerably shorter than the large intestine; the proportions in three specimens respectively: 443 to 613; 453 to 502; and 420 to 478 mm. The diameter of the small intestine is, for most of its length, greater than that of the large intestine.

*Liver and pancreas*.—Liver divided into six lobes. No gall bladder in pocket gophers, nor in kangaroo rats. Largest lobe, left lateral; right lateral lobe next in size to left; right and left central lobes subequal. Central lobes incompletely divided by fissure in which falciform ligament attaches. Caudate lobe divided into several processes. Extends in caudal direction on dorsal body wall, lying on right kidney. Vena cava inferior enters dorsomedial surface of caudate lobe. Portal vein runs ventral to main part of lobe and dorsal to smaller, flattened lobule which lies in lesser omentum and reaches to lesser curvature of stomach. This lobule lies to left of portal vein and bile duct; small process projects caudad, dorsal to portal vein, and forms right margin of small foramen epiploicum. The liver is subject to a little individual variation in relative shape and size of its lobes. It is similar in both genera of pocket gophers and also in the heteromyine forms, *Dipodomys*, *Microdipodops*, and *Perognathus*.

*Pancreas* (fig. 25) a diffusely scattered, glandular mass lying in mesoduodenum, mesocolon, and greater omentum. Single duct present which unites with common bile duct and enters duodenum with it.

The intestinal tract in pocket gophers is quite similar to that in the Heteromyinae, but is unlike that in other rodents in exhibiting a paracaecal loop. The squirrels and *Apodonta* exhibit large right and left colic loops, whereas most muroid forms possess a spiral coil near

the caecum (Bonfert, 1928; Mitchell, 1905, 1916). The condition of the colon in *Castor* (Tullberg, 1899) is most nearly like that in the geomyoid rodents, but this resemblance may be convergent.

### RESPIRATORY SYSTEM

*Nasal cavities and passage.*—The bony nasal cavity was described by Merriam (1895) and figured by him. In the flesh the nasal cavity is similar except for the mucosa which lines it, and the more extensive cartilaginous septum.

*Larynx.*—Hardly larger in diameter than trachea; vocal ability of pocket gopher restricted. A strong hissing is only noise usually made, but I have heard squeals somewhat like those made by a trapped ground squirrel. Laryngeal opening large, roughly triangular. Epiglottis diamond-shaped. Laryngeal opening bounded laterally by well-marked aryteno-epiglottic folds. Vestibular folds vestigial, short V-shaped folds at base of the epiglottis; vocal folds absent; glottis margined by elongate arytenoid cartilages covered by laryngeal mucosa. Arytenoid cartilages do not reach ventral wall of larynx, leaving a semicircular passage ventral to glottis. Latter narrow and slitlike.

Thyroid cartilage semicylindrical, without ventral prominence. About same size as cricoid cartilage which lies caudal to it and which forms complete ring around larynx. Arytenoids narrow, elongate in ventral direction; articulate with cricoid cartilage as usual. Single epiglottic cartilage present. Trachea exhibits no characters of particular interest.

Thyroid gland consists of two fusiform lobes situated one on either side of trachea, caudal to larynx, deep to sternothyroid muscle. Isthmus appears to be absent in pocket gophers as far as could be made out with dissecting microscope. Thyroid gland exhibits usual granular appearance.

Left lung undivided as Tullberg (1899) found to be true in *Geomys tuza*. Right lung exhibits usual three main lobes and large, independent mediastinal lobe. Latter projects into special pleural pocket formed by caval fold supporting postcava vein. Left lung fused in murid rodents and in heteromyine genera, but in none of the sciurids or their relatives.

Mediastinal lobe smallest of lobes in right lung, next to it in size is cephalic lobe, and basal lobe is largest. Right lung larger than left.

### CIRCULATORY SYSTEM

The circulatory system was investigated in several injected specimens each of *Thomomys bottae* and *Geomys bursarius*. Certain features of particular interest were also examined in *Aplodontia*, *Citellus*, *Sciurus*, *Neotoma*, and *Rattus*.

*Heart.*—In pocket gophers, pericardium completely separated from diaphragm, except where attached by mediastinal septum and caval fold. Part of its ventral side remains unseparated from ventral body wall. This is so in the murids also, but in the other rodents examined the pericardium is excluded from the ventral body wall by the pleural cavities, and is attached only by the ventral mediastinal septum.

Atria small with relatively large auricles; heart otherwise not noteworthy.

### ARTERIES

(Fig. 26)

*Pulmonary artery.*—Exhibits relations similar to this vessel in the cat (Reighard and Jennings, 1930). Although the left lung is a single lobe in pocket gophers, the pulmonary artery on the left side sends a large branch to the region of the upper lobe in other mammals—indicative of a primitive division of this lung.

*Aorta.*—Of the usual mammalian type, as are the two coronary arteries which spring from its base. Arch of aorta gives off three vessels: innominate, left common carotid, and left subclavian. This condition is the primitive mammalian arrangement, since the innominate artery represents the base of the right fourth aortic arch. In *Neotoma* and *Rattus* (cf. Hunt, 1924; Starks and Cutter, 1931), also in *Aplodontia*, conditions are as in pocket go-



phers; Parsons (1902) described the same condition in *Gerbillus* and *Castor*. In *Citellus* and *Sciurus*, however, the left common carotid arises from the innominate (cf. Parsons, 1902; Sleggs, 1925).

*Common carotid artery*.—Runs cranial along trachea, closely associated with vagus and sympathetic nerves, and internal jugular vein. Usually gives off, in *Thomomys*, inferior laryngeal artery, slightly caudal to larynx. This more normally arises from thyrocervical trunk, and came off from that vessel in some specimens of *Thomomys* and *Geomys*. It supplies *M. longus colli*, trachea, esophagus, thyroid gland, and larynx.

Opposite caudal end of larynx, common carotid gives off superior thyroid artery. This supplies thyrohyoid and cricothyroid muscles, thyroid gland, and larynx; it continues into sternohyoid muscle; runs caudad between its fibers as far as the sternum.

*Internal carotid artery*.—Cranial to origin of superior laryngeal artery, common carotid divides into internal and external carotid arteries. Former runs dorsad as far as tympanic bulla, enters cranium through small foramen between anterior end of bulla and basisphenoid. It runs forward to infundibulum where it joins arterial circle. Stapedial artery, large and important in other rodents, with exception of *Aplodontia*, is obsolete in pocket gophers and pocket mice. In pocket gophers a ligament connects internal carotid with obliterated stapedial foramen.

*External carotid artery*.—Runs cranioventrad. Near level of hyoid bar small vessels are given off to pharynx, a lingual artery to tongue, and external maxillary artery to lower facial region. External maxillary passes to lateral side of lower jaw; runs along ventral border of superficial masseter muscle with anterior facial vein. A branch runs obliquely cranio-dorsad, deep to superficial masseter, then along its dorsal border. Both branches supply superficial muscles and skin of face.

External carotid then divides into internal maxillary and a short common trunk to muscles of neck and to temporal region.

Internal maxillary turns dorsad and runs near tympanic bulla, ventrolateral to course of internal carotid. Near anterior end of bulla it lies medial to lateral pterygoid plate. Here middle meningeal artery passes dorsad into cranial cavity through foramen ovale. From opposite side of internal maxillary, inferior alveolar artery arises; accompanies inferior alveolar nerve to mandibular foramen; supplies lower jaw and muscles of floor of mouth. Internal maxillary, after giving off these branches, enters alisphenoid canal with masticatory nerve. In canal, medial branch arises to supply internal pterygoid muscle. Slightly anterior to this a lateral branch, deep temporal artery, passes through masticatory foramen to temporal muscles and to medial masseter.

Internal maxillary artery emerges into orbit through sphenorbital fissure. Palatine artery arises opposite palatine canal; passes to palate through greater palatine canal; runs in deep palatal groove. Nasal branch of palatine enters incisive foramen. Another branch passes with its fellow through minute interpremaxillary foramen behind upper incisors. These supply anterior part of nasal cavity.

In orbit internal maxillary artery gives off branch to muscles of eyeball; another branch (sphenopalatine artery) enters nasal cavity by sphenopalatine foramen. Main branch, infra-orbital artery, enters infraorbital canal; supplies alveolus of incisor; emerges on rostrum; supplies buccinator muscle; other branches anastomose with terminal twigs of external maxillary artery.

*Arteries of brain*.—Vertebral artery (branch of the subclavian) passes into vertebral canal through first intervertebral foramen, caudal to, rather than cranial to, atlas. Runs ventrad and mediad, uniting with its fellow under medulla oblongata, just anterior to foramen magnum, to form basilar artery. Small branches from vertebral and basilar arteries supply medulla. Basilar artery runs forward to infundibular region; divides to form posterior cerebral arteries of arterial circle. This is irregularly hexagonal; basilar artery enters at posterior angle, internal carotids come in on parallel sides. Posterior communicating arteries large; sides of figure subequal.

Two cerebellar arteries, given off from caudolateral angles of arterial circle, supply cerebellum. Anterior to these, posterior cerebral arteries arise from circle; run in deep fissure

Anterior to junction of internal carotid with arterial circle, small anterior choroideal artery arises; runs dorsal along optic tract; supplies choroid plexus of third and lateral ventricles and adjacent structures.

Middle cerebral arteries arise from anterolateral angles of arterial circle; and run dorsal on cerebrum, branching profusely. Anterior communicating arteries short; anterior cerebrals close together. Latter run cranial along olfactory tract, supplying olfactory lobes and frontal region of cerebrum.

*Subclavian artery*.—Right subclavian artery arises from innominate opposite first rib; left subclavian from arch of aorta. Both have identical branches. Near first rib, subclavian artery divides into six vessels: vertebral, thyrocervical trunk, axillary, thoracocervical, internal mammary, and superior intercostal. Latter two may come off from common short trunk; axillary and thoracocervical may be united for a short distance.

*Vertebral artery*.—Turns dorsomedial; enters transverse foramen of sixth cervical vertebra. Runs cranial in vertebralarterial canal of neck, supplying branches to spinal medulla and to deep muscles of neck; accompanies second spinal nerve, caudal to atlas, to vertebral canal. Endocranial course described above.

*Thyrocervical trunk*.—Runs obliquely cranio-lateral for short distance; divides into inferior thyroid and transverse scapular arteries. Former may divide again into inferior laryngeal and ascending cervical vessels, or inferior laryngeal artery may arise from common carotid (described above, p. 144). Ascending cervical runs along ventral margin of M. scalenus, supplying this and M. longus capitis. Opposite second cervical vertebra large branch arises; supplies sternocleidomastoid group of muscles and omocervicalis. Here ascending cervical turns dorsocaudal; ends by supplying clavicular part of trapezius. Transverse scapular artery runs to point of shoulder. Here three branches given off: one follows supraclavicular nerve to skin of shoulder; one accompanies external jugular vein to parotid gland; one passes to cephalic part of M. subscapularis. Several millimeters beyond this, transverse scapular artery gives off large branch to lateral surface of M. supraspinatus which runs along spine of scapula with accessory nerve, branching to Mm. supraspinatus, trapezius, and occipitoscapularis. Transverse scapular turns mediodorsal; follows supra-scapular nerve to lateral surface of scapula; supplies Mm. supraspinatus and infraspinatus.

*Thoracocervical trunk*.—Arises from caudal side of subclavian artery; divides into deep cervical and lateral thoracic arteries. Latter vessel passes out of thoracic cavity in first intercostal space; accompanies long thoracic nerve across surface of serratus anterior. Soon after emerging from thorax, large branch arises; pierces serratus anterior; runs to vertebral border of scapula; divides; sends branches to Mm. levator scapulae, rhomboideus, serratus posterior superior, and longissimus.

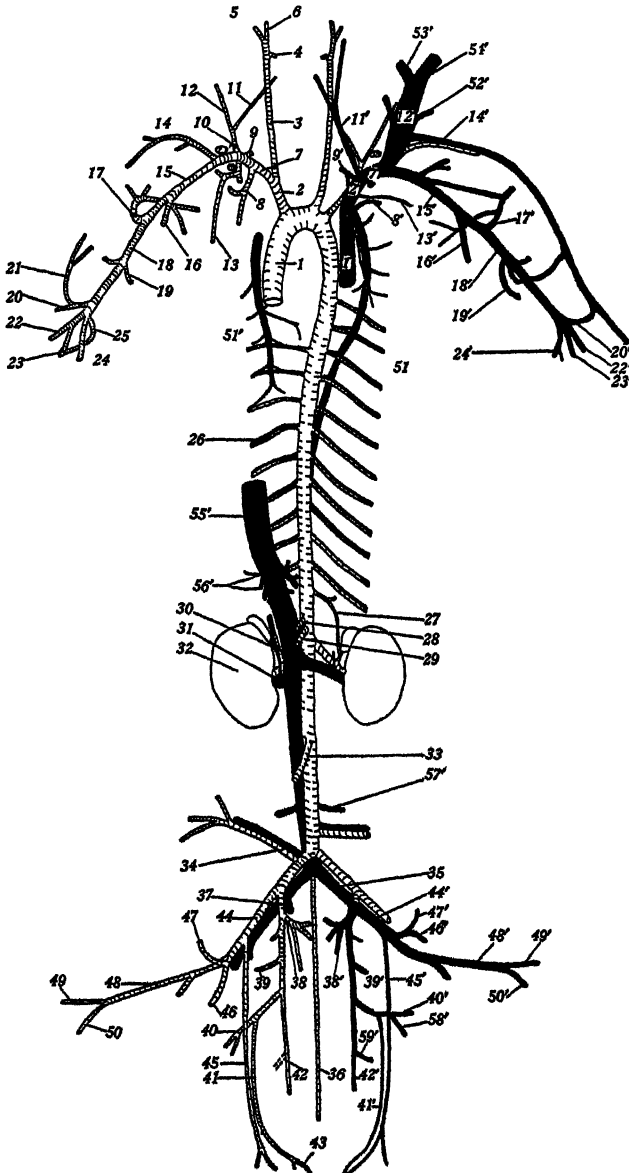
*Superior intercostal*. On left side supplies dorsal part of first two or three intercostal spaces; on right side, the first five. Other branches supply vertebral and epaxial muscles of cranial part of thorax.

*Internal mammary*.—Runs to ventral thoracic wall, then parallel with sternum, some 8 mm. laterally from midline. Gives off ventral intercostal arteries which anastomose with dorsal intercostals. Supplies parts of Mm. scalenus and rectus abdominis, marginal region of diaphragm, and muscles of ventral part of thoracic wall.

*Axillary artery*.—Largest branch of subclavian artery. Passes over first rib with subclavian vein and lower trunk of brachial plexus. Just lateral to rib, thoracoacromial artery arises from ventral side; passes to clavicle with external jugular vein; accompanies cephalic vein to insertion of deltoid; supplies Mm. subclavius, pectoralis, and deltoideus. About 7 mm. lateral to origin of above vessel, large anterior thoracic artery arises; runs to caudal margin of M. pectoralis minor, branching to this and pectoralis major. Large branch (external mammary) runs along dorsal margin of pectoralis abdominalis, supplying this muscle and cutaneous maximus. In females, external mammary supplies pectoral mammary glands also.

Slightly lateral to origin of anterior thoracic artery, axillary gives off large subscapular branch. This passes to M. subscapularis near glenoid angle of scapula; divides into posterior humeral circumflex, thoracodorsal, and several small subscapular vessels. The first

passes through quadrilateral space between *Mm.* subscapularis, teres major, and triceps longus, and head of humerus. Accompanying axillary nerve, posterior circumflex artery reaches lateral side of shoulder. Here it supplies by numerous branches *Mm.* deltoideus, teres minor, infraspinatus, and triceps. In the quadrilateral space a branch arises; supplies *Mm.* biceps and coracobrachialis. Thoracodorsal artery runs along axillary border of scapula, giving off several minor branches; near middle of axillary border it gives off large circumflex scapular branch; then passes to surface of *M.* latissimus dorsi, where it ends. Circumflex scapular artery continues along vertebral border of scapula, almost to caudal angle, branching to *Mm.* latissimus dorsi, teres major, and subscapularis. Near the angle, it passes to lateral side of scapula where it supplies *M.* infraspinatus, *M.* spinotrapezius, and that part of *M.* serratus anterior adjacent to caudal angle.



**Brachial artery.**—Continuation of axillary in upper arm. In proximal third of course, branch given off to *M. biceps*. Large deep humeral artery arises from opposite side; passes between long and medial heads of triceps to lateral side of arm; gives off branches to triceps, then accompanies radial nerve to elbow; supplies brachialis and biceps; then becomes superficial artery of forearm, running with superficial branch of radial nerve and with cephalic vein. On dorsum of hand this vessel unites with dorsal arch.

Near elbow, brachial artery divides into three branches: radial, ulnar, and superficial ulnar. Radial artery not as important as in man; passes, superficial to median nerve, to surface of *M. biceps* near its insertion. Here several branches arise, one of which (radial recurrent artery) runs back almost to shoulder with cephalic vein. Radial artery passes to surface of *M. pronator teres*; divides into two branches. Superficial branch runs along medial surface of flexor muscles, supplying these and skin; supplies radial side of wrist; anastomoses with dorsal carpal arch. Deep branch runs between flexor carpi radialis and extensores carpi radialis, supplying these muscles and radial head of flexor digitorum profundus. Follows tendon of flexor profundus into manus.

Ulnar artery large; passes deep to median nerve; near elbow joint gives off two branches: median and dorsal interosseous arteries. It then runs caudad to the ulnar nerve, deep to condylar flexor muscles, supplying these and deep flexor muscles; accompanies ulnar nerve to wrist; branches to skin on ulnar side; unites with dorsal carpal arch. This arch formed by terminal branch of superficial artery of the forearm, which anastomoses with ulnar and superficial radial arteries. A branch goes to radial side of pollex, another to ulnar side of fifth digit, and four metacarpal arteries, one to each interdigital cleft. Each metacarpal artery divides; a branch runs along each margin of each cleft.

Median artery accompanies median nerve, branching to muscles adjacent thereto. Near wrist it emerges between flexor carpi radialis and flexor digitorum profundus; accompanies tendon of latter into hand. No volar carpal arch; median artery branches to each digit in a manner similar to that of dorsal arch.

Dorsal interosseous artery runs laterad, passing between radius and ulna near elbow joint. Supplies *Mm. anconeus* and *supinator*; divides into two vessels, one running along cranial margin of extensor pollicis longus, the other along caudal border. Branches supply this and other extensor muscles of forearm.

Superficial ulnar artery runs on medial surface of medial epicondyle. Soon after origin, gives off ulnar collateral artery to insertion of *M. triceps* and to *M. epitrochleo-anconeus*. Branch of ulnar collateral accompanies ulnar nerve into forearm, anastomosing with ulnar artery. Superficial ulnar continues along epicondylar ridge, running between epitrochleo-anconeus and condylar flexor muscles. Caudal to latter muscles, turns distad and runs between *M. palmaris longus* and *M. flexor carpi ulnaris*; supplies these and adjacent muscles, and skin.

Fig. 26. Circulatory system (*Thomomys bottae*),  $\times 1\frac{1}{4}$ . 1, aorta; 1', V. cava superior; 2, 2', A. and V. anonyma; 3, A. carotis communis; 4, A. thyroidea superior; 5, A. carotis interna; 6, A. carotis externa; 7, 7', A. and V. subclavius; 8, 8', A. and V. mammaria interna; 9, 9', A. and V. vertebralis; 10, A. thyrocoervicalis; 11, A. thyroidea inferior (may arise from common carotid); 11', V. jugularis interna; 12, A. cervicalis ascendens; 12', V. jugularis externa; 13, 13', A. and V. thoracica longa; 14, A. thoracoacromialis; 14', V. cephalica; 15, 15', A. and V. axillaris; 16, 16', A. and V. thoracica ventralis; 17, 17', A. and V. subscapularis; 18, 18', A. and V. brachialis; 19, 19', A. and V. profunda brachii; 20, 20', A. and V. radialis; 21, A. radialis recurrens; 22, 22', A. and V. media; 23, 23', A. and V. ulnaris; 24, 24' A. and V. ulnaris superficialis; 25, A. ulnaris collateralis; 26, Aa. and Vv. intercostales; 27, A. phrenica; 28, A. coeliaca; 29, A. mesenterica superior; 30, A. and V. suprarenalis; 31, A. and V. renalis; 32, kidney; 33, A. mesenterica inferior; 34, A. and V. iliolumbalis; 35, A. and V. iliaca communis; 36, A. sacralis media; 37, A. and V. hypogastrica; 38, 38', A. and V. umbilicalis; 39, 39', A. and V. glutea superior; 40, 40', A. and V. glutea inferior; 41, 41', A. and V. pudendis; 42, 42', ventral rami of A. and V. hypogastrica; 43, 43', A. and V. dorsalis penis; 44, 44', A. and V. iliaca externa; 45, 45', A. and V. epigastrica inferior; 46, 46', 47, 47', A. and V. circumflexa iliaca profunda; 48, 48', A. and V. femoris; 49, 49', A. and V. poplitea; 50, 50', A. and V. saphena; 51, V. hemiazgygos; 51', V. azygos; 52', V. transversa scapulae; 53', V. facialis anterior; 54' V. facialis posterior; 55', V. cava inferior; 56', V. hepatis; 57', V. ovaria; 58', V. femoris lateralis superficialis; 59', V. obturatorius.

*Thoracic aorta.*—Runs in mediastinum with esophagus and hemiazygos vein. In *Geomys*, azygos vein also accompanies aorta. Eight to ten intercostal arteries given off, and one or two subcostals depending on number of ribs. When twelve ribs, two subcostal arteries; when thirteen ribs, one. This may be taken to indicate that the primitive number of ribs was thirteen. Near heads of ribs, intercostal arteries give off dorsal branches which accompany dorsal (posterior) rami of spinal nerves to epaxial muscles. Along caudal margin of each rib, intercostal artery lies beside ventral ramus of nerve; supplies branches to muscles of thoracic wall. Each ends by anastomosing with ventral intercostal branch of internal mammary artery. Subcostal arteries follow courses similar to intercostals, but supply abdominal wall.

An unpaired artery arises from thoracic aorta near fourth thoracic vertebra; runs in mediastinal septum to esophagus; follows digestive tract almost to diaphragm.

Left phrenic artery may arise in thorax or in abdominal cavity. Supplies crura of diaphragm; usually anastomoses with phrenic branch of suprarenal artery. Right phrenic comes off from right suprarenal artery.

*Abdominal aorta.*—Runs in midline to pelvic region.

*Coeliac artery.*—First branch of aorta in abdominal cavity, unless, as in some individuals, phrenic comes off more caudally than usual. Runs caudoventrad in dorsal mesentery; some 6 mm. from origin divides into two branches, hepatic artery and short common trunk which again divides into left gastric and splenic arteries. These two vessels may, more rarely, arise separately.

Hepatic artery runs to right and cranial, accompanying portal vein toward liver. Near porta hepatis small vessel goes to liver, but larger branch, gastroduodenal artery, turns and runs with bile duct caudoventrad in hepatoduodenal ligament. Near pylorus, gastroduodenal divides into three branches: superior pancreaticoduodenal, right gastric, and right gastroepiploic. Latter vessel may arise from either of other two. Right gastric artery supplies pylorus; right gastroepiploic runs along greater curvature of stomach, branching to walls; superior pancreaticoduodenal artery supplies duodenum between pylorus and entrance of bile duct, and adjacent part of pancreas.

Large left gastric artery passes to lesser curvature of stomach; supplies end of esophagus and greater part of stomach. Splenic artery gives off a large short gastric artery to cardiac part of stomach and a number of pancreatic branches to pancreas in greater omentum and mesocolon. It then divides into right and left splenic arteries, which enter spleen.

The spleen is triangular. It lies in poorly developed greater omentum, between stomach and left colic loop. Triangular shape relatively constant in pocket gophers of both genera, but size varies considerably.

*Superior mesenteric artery.*—Arises from aorta immediately caudal to coeliac, or may come off with coeliac from common trunk. Runs caudad and ventrad in mesoduodenum. Near origin gives off middle colic artery to transverse colon. Some 5 mm. caudad, superior mesenteric artery gives off inferior pancreaticoduodenal branch. This divides into two branches, one running transversely to supply descending duodenum, the other running obliquely to transverse and ascending parts; both supply the pancreas in the mesoduodenum.

Varying number of intestinal arteries arise from superior mesenteric and run to jejunum. Intestinal branches all arise from left side of artery, morphologically the cranial side. Right colic artery arises from opposite side of superior mesenteric; passes ventrad to duodenum; runs to right colic loop. Caudal to this, superior mesenteric sends a branch to cranial part of paracaecal colic loop. Terminal branch of superior mesenteric, ileocaecocolic artery, passes to dorsal surface of caecum; supplies this, ileum, and paracaecal loop of colon.

In *Geomys*, except that there is an additional paracaecal artery, branches of the superior mesenteric are similar to those in *Thomomys*.

*Inferior mesenteric artery.*—Arises from aorta opposite fourth lumbar vertebra; passes ventrad in mesocolon. Near colon, divides into left colic artery and superior hemorrhoidal. Former branches to left colic loop and proximal part of colon descendens, anastomosing with left branch of middle colic artery. Superior hemorrhoidal runs caudad in mesocolon

supplying distal end of descending colon; continues into middle hemorrhoidal artery in pelvis; bifurcates; runs on sides of rectum. Hemorrhoidal artery ends by branching to rectum near anal sphincter. There is no anastomosis with the hypogastric artery in the specimens examined, although it was looked for carefully.

*Renal arteries.*—Arise from abdominal aorta, about opposite each other, several millimeters caudal to base of coeliac artery. Either may be slightly in advance of other. Near kidney, slender suprarenal artery arises from renal; supplies suprarenal gland and diaphragm. On left side this vessel usually anastomoses with superior phrenic branch of aorta; on right side latter vessel absent. Internal spermatic artery was not found in male specimens examined (four), and in only one female was there a true ovarian artery. This was on left side; it arose from aorta approximately halfway between renal and ilio-lumbar arteries.

*Lumbar arteries.*—One to each segment. Branch to muscles of back and to bodies of vertebrae, where are large nutrient foramina. One lumbar artery arises from aorta opposite each vertebra.

*Iliolumbar arteries.*—Left ilio-lumbar artery cranial to one on right side, arising from aorta opposite last lumbar vertebra. Right artery comes off from common iliac; branches of two alike. Iliolumbar runs transversely across psoas and iliacus muscles which it supplies. Near lateral body wall a large branch runs cranial on abdominal surface of *M. sacrospinalis*, supplying it; extends forward to level of kidney. Iliolumbar then gives off branch to body wall; passes through abdominal muscles to exterior; accompanies iliohypogastric nerve to inguinal fat and, in females, to inguinal mammary glands. Branch to body wall runs between transverse abdominal muscle and internal oblique; anastomoses with last subcostal artery and with branches of deep circumflex iliac artery.

Opposite caudal end of last lumbar vertebra, aorta divides into two common iliac arteries and median sacral. In one specimen median sacral artery arose from left common iliac. Accompanied by median sacral vein, the artery runs entire length of tail in midventral line, branching to muscles and integument of tail. Common iliac runs obliquely caudolaterad; at level of joint between first two sacral vertebrae divides into external iliac and hypogastric arteries.

*Hypogastric artery.*—Runs dorso-caudad from its origin. Umbilical artery arises from ventral side; runs in mesorehium or mesometrium as case may be. In males, umbilical divides into three branches: arteria deferentialis, accompanying ductus deferens; vesical artery, supplying lateral side of bladder; false spermatic artery, supplying testis. In females, vesical artery similar, but the other branch supplies uterus, ovary, and vagina, so that it seems to correspond to both deferential and false spermatic arteries. Internal spermatic and ovarian arteries usually absent; their functions are taken over by false spermatic and uterine vessels.

Branch of hypogastric artery arises from ventral side near iliopectineal eminence; passes deep to tendon of psoas minor; supplies distal part of *M. psoas major*. Large, dorsal superior gluteal branch arises at this level; passes through cranial end of greater sciatic foramen with superior gluteal nerve. It branches to muscles supplied by this nerve and to proximal part of rectus femoris. Several millimeters caudal to this, hypogastric artery divides into dorsal and ventral rami. Dorsal ramus passes through caudal end of greater sciatic foramen; divides into inferior gluteal and pudendal arteries. Former supplies *Mm. gluteus maximus* and *femorocoechygeus*; branch accompanies posterior cutaneous nerve of thigh to skin; branch supplies proximal third of hamstring muscle mass.

Pudendal artery runs with pudendal nerve caudad along dorsal margin of ischium to dorsal tuberosity. Turns ventrad; passes between *M. pubocoechygeus* and crus penis; divides into deep artery of penis, which enters crus, and dorsal artery which runs on dorsolateral side of penis, separated from its fellow by medial dorsal vein. Description applies to males; in females, however, vessels are similar in courses and relations. Ventral ramus of hypogastric artery supplies endopelvic muscles; obturator internus, iliocoechygeus, and pubocoechygeus. In *Geomys*, obturator artery accompanies obturator nerve to leg; absent in *Thomomys*, its function seemingly taken over by branch of deep femoral artery. Obturator vein present; accompanies this branch of deep femoral artery in distal part of course.

*External iliac artery.*—Continues in caudolateral direction from origin; crosses ventrally over hip bone. Inferior epigastric branch arises from caudal side; accompanies genitofemoral nerve along ventral margin of pubis; near middle of pubis divides into three branches: One follows inguinal nerve to muscles of ventral body wall; another anastomoses with obturator artery, when present; third branch, pubic ramus, continues caudad. Near symphysis this divides into several branches which supply *M. rectus abdominis*, fat of inguinal and perineal regions, and lateral side of penis or clitoris, ending in preputial glands. In females a terminal branch supplies inguinal mammary glands also.

As external iliac passes dorsally under inguinal ligament, gives off large deep circumflex iliac artery to abdominal wall. This runs between *Mm. transversus abdominis* and *obliquus internus*, branching treelike. Branches anastomose with those of inferior epigastric, iliolumbar, and subcostal.

*Femoral artery.*—Direct continuation of external iliac in leg. Some five millimeters after passing out of abdominal cavity, gives off large deep femoral. This passes between *psaos major* and *pectineus*, branching to these muscles, *obturator externus*, and *adductores*. Small twigs arise from each side of femoral in the thigh, supplying muscles on medial surface. Near insertion of *M. iliacus*, lateral circumflex femoral artery arises from cranial side; supplies proximal part of *extensor quadriceps*. Near middle of thigh, large branch runs caudad and proximad on medial surface, branching to *Mm. adductores* and *gracilis*; continues to fat of perineal region, passing deep to *M. gracilis*. This artery, although present in the cat (Reighard and Jennings, 1930, p. 310, fig. 127), seems to have no counterpart in man.

Femoral then divides into three branches: great saphenous, popliteal, and superior geniculate. The last is the smallest; supplies distal parts of *rectus femoris* and *vastus medialis*. Great saphenous artery runs over medial surface of leg with great saphenous vein, much as in the cat. Branches supply distal parts of *Mm. caudofemoralis* and *semimembranosus*, inguinal fat body, and, in females, inguinal mammary glands. Below knee, inferior geniculate artery passes to knee joint; another branch supplies distal end of *M. semitendinosus*. Near middle of leg, great saphenous artery divides into dorsal and plantar rami. Dorsal branch passes to dorsum of foot, plantar branch to sole. Both unite with tarsal arterial arches described below.

*Popliteal artery.*—Largest terminal branch of femoral. Shortly after its origin, a branch arises which pierces *adductor brevis* and runs between this muscle, *adductor magnus*, and hamstrings proximad almost to hip bone. Popliteal artery passes through triangle formed by *caudofemoralis*, *adductor magnus*, and medial condyle of femur, and comes to lie on surface of *M. popliteus*. Here branch given off to *M. biceps* and deep surface of *M. semitendinosus*. Another branch supplies *M. popliteus*. Several small arteries pass to back of knee joint and to distal end of femur. Small saphenous artery arises from popliteal and runs down lateral surface of *M. gastrocnemius*, accompanied by vein. Passes to plantar surface of foot; anastomoses with posterior tibial and with plantar branch of great saphenous artery to form plantar arch.

Several small sural arteries arise from popliteal, supplying proximal part of *gastrocnemius*, *plantaris*, and *soleus* muscles. Another branch follows common peroneal nerve and supplies peroneal group of muscles. Popliteal artery then passes between heads of *M. gastrocnemius* and divides into anterior and posterior tibial arteries. Latter vessel runs distad, between *gastrocnemius* and *flexores digitorum*, branching to all flexor muscles of leg. Slender terminal branch continues to medial side of heel. Here gives off twig to heel and crosses to join small saphenous artery on lateral side of plantar arch.

*Plantar arterial arch.*—Roughly U-shaped, convexity directed distally. Formed as mentioned above by union of small saphenous, posterior tibial, and plantar branch of great saphenous artery. Gives off six branches: one to medial side of hallux, one to lateral side of fifth digit, and one (metatarsal artery) to each interdigital cleft, as in dorsal arch of hand. Metatarsal arteries divide into branches that run along margins of interdigital clefts, branching to digits concerned.

*Anterior tibial artery.*—Pierces interosseous membrane and immediately gives off large peroneal artery. Latter runs along anterior margin of peroneus longus, supplying peroneal muscles and extensor digitorum longus; follows tendon of extensor digitorum longus to dorsal surface of foot and divides, supplying fifth digit and fourth interdigital cleft. Usually anastomoses with posterior tibial artery. Anterior tibial artery runs deep to M. tibialis anterior along with deep peroneal nerve. On dorsum of foot unites with dorsal branch of great saphenous artery and with posterior tibial artery. Branches supply three medial interdigital clefts and medial side of hallux.

## VEINS

(Figs. 25 and 26)

*Pulmonary veins.*—Two from left lung, four from right lung, unite to form single pulmonary vein, immediately before emptying into left atrium.

Three large systemic veins enter right atrium: two superior venae cavae (precavae), and inferior vena cava (postcava).

*Superior venae cavae.*—Collect blood from prediaphragmatic part of body. External jugular vein from head, neck, and shoulders; small internal jugular from thyroid gland and neck; axillary vein from pectoral limb; and several veins from thoracic body wall, all unite to form these vessels. The veins will be traced toward the heart, in the direction of the flow of blood.

*Posterior facial vein.*—External nasal vein collects blood from region of external nares and rostrum; anastomoses with anterior facial vein deep to facial muscles of mouth. Near orbit, branches from maxillonasalis and maxillolabialis muscles are received, and vein passes around dorsal margin of orbit as supraorbital vein. Supraorbital receives small branches from orbit and from nutritive foramina of premaxillary and frontal bones. At caudolateral angle of orbit a relatively large vessel from orbit enters supraorbital. Latter then unites with zygomatic vein to form superficial temporal vein, and small anterior auricular vein, from anterior side of ear and from preauricular muscle, is received. Zygomatic vein runs along zygomatic arch, receiving branches from masseter muscle and from orbit.

Ventral and slightly medial to external ear opening, superficial temporal unites with large postglenoid vein, emerging from cranial cavity through the postglenoid foramen to form posterior facial vein. In pocket gophers the postglenoid is the chief vessel draining the brain; it connects with the transverse sinus near the rudimentary tentorial ridge. Into this empties posterior auricular vein, from region caudal to ear and from Mm. platysma and sphincter colli primitivus. Parotid and internal maxillary veins also unite with posterior facial.

Large internal maxillary vein begins in orbit, receiving blood from plexus of sinusoid veins surrounding eyeball. Anastomosing vein passes through presphenoid foramen (there are two anastomosing vessels in *Geomys bursarius*). Other vessels accompany corresponding branches of internal maxillary artery: sphenopalatine, infraorbital, and palatine veins. In pocket gophers, internal maxillary vein does not run in sphenopterygoid canal as in other rodents, but runs on lateral surface of alveolar part of maxilla, deep to masseter muscles. Several large tributaries from these and M. temporalis are received. Internal maxillary vein runs between internal and external pterygoid muscles; between digastric and ramus of mandible, to emerge behind lower jaw. Unites with posterior facial several millimeters ventral to commencement of that vein. Posterior facial vein runs ventrocaudad in parotid gland, and opposite angle of jaw unites with anterior facial vein to form external jugular.

*Anterior facial vein.*—Arises in ventral part of rostrum, from union of a number of small vessels draining Mm. buccinator and orbicularis oris. Runs along ventral border of superficial masseter muscle. Opposite angle of jaw, transverse vein connects anterior facial veins of both sides of head. Anastomoses with internal jugular vein in some specimens. Besides, anterior facial vein receives branches from digastric muscle and from ventral slip of platysma. Anterior facial then runs caudad into parotid gland, where it unites with posterior facial to form external jugular vein.



*External jugular vein* (fig. 18).—Runs on lateral surface of sternomastoid muscle, caudad and ventrad, entirely superficial to neck muscles and to clavicle. Small branches from neck empty into external jugular and after passing ventral (superficial) to clavicle, it receives cephalic vein from arm.

*Cephalic vein* (fig. 18).—Begins on dorsum of manus, collecting blood from dorsal venous arch, which is similar to arterial arch. Several vessels accompany superficial artery up cranio-lateral surface of forearm and unite near elbow. Here a large vein emerges from between Mm. triceps and biceps, collecting branches from these and from extensor group of forearm, anastomosing with profunda vein and with brachial. Near insertion of deltoid, cephalic vein receives large basilic vein. This vessel collects blood from flexor aspect of forearm and from muscles on medial side of upper arm. At elbow, basilic anastomoses with brachial vein. After uniting with the basilic, cephalic vein runs in groove between deltoid and pectoral muscles, accompanying thoracoacromial artery. Near sternum, cephalic and external jugular veins unite and pass between sternum, clavicle, and pectoral muscles. Transverse scapular vein accompanies thyrocervical artery; enters external jugular, running deep to clavicle. External jugular then unites with axillary vein to form subclavian.

In *Apodonta* and in *Citellus* (cf. Sleggs, 1925), the external jugular vein forms a circle around the clavicle. Only the deep part of this circle is present in *Sciurus*; it corresponds to the lower part of external jugular vein in man; only the ventral part of the circle is present in pocket gophers, in *Neotoma*, and in *Rattus*. Possibly the condition in *Apodonta* and *Citellus* is primitive for rodents, since both types of external jugular veins may be derived therefrom.

*Axillary vein*.—The veins of the pectoral limb, with the exception of the cephalic and basilic which have been described, accompany the arteries closely. Usually there is only a single vena comitis with each artery, but there may be two. The only tributary of the axillary vein not accompanying an artery is one of the subscapular veins. This runs back from quadrilateral space at medial side of shoulder joint, along with axillary nerve, and empties into axillary vein opposite place where ventral thoracic vein joins that vessel.

*Subclavian and vertebral veins*.—Subclavian unites with internal jugular, vertebral, and small branch from thymus gland. Vertebral vein runs in vertebralarterial canal along with artery, collecting blood from neck muscles, spinal medulla, and vertebrae. Emerges from foramen transversarium of sixth cervical vertebra, joined by thoracocervical vein from serratus group of muscles and neck. Internal jugular vein small, and may not reach head. Usually drains thyroid gland and trachea, and some neck muscles. In some specimens it begins in cranium, emerges through jugular foramen; it may anastomose with transverse facial near level of hyoid bone.

Subclavian runs caudad; opposite first rib receives internal mammary vein from ventral thoracic wall and slender pericardiophrenic vein that runs with phrenic nerve from diaphragm. Few millimeters caudal to entrance of these veins, right subclavian unites with azygos, left subclavian with hemiazygos, to form superior vena cavae.

*Azygos and hemiazygos veins*.—In *Thomomys*, azygos is reduced, but in *Geomys* it is subequal with hemiazygos. In the former genus, azygos vein may collect from first three intercostal spaces only, but in some specimens drains as many as eight. It lies, in *Thomomys*, on dorsal body wall near angles of ribs, but in *Geomys* lies nearer dorsal aorta and receives vein from esophagus as well as right intercostal branches. In *Thomomys*, hemiazygos is the more important vessel, as in *Castor* (Beddard, 1907) *Rattus* (Hunt, 1924; Starks and Cutler, 1931), and also, as I found, in *Neotoma*. On the contrary, the azygos vein is developed to the exclusion of the other vessel in squirrels (cf. Beddard, 1907; Sleggs, 1925) and, as I determined, in *Apodonta*. Hemiazygos lies lateral to and near dorsal aorta and, in *Thomomys*, receives veins of left intercostal spaces and last three to eight right intercostal veins, also esophageal vein. Several more cephalic intercostal veins on left side may empty into innominate directly. There are eleven or twelve dorsal intercostal veins and one or two subcostals. First of these latter vessels, when both are present, enters hemiazygos vein. Second (or only) subcostal drains into postcava.

The cardiac veins in pocket gophers are apparently not homologous to those in man. Left cardiac vein arises near apex of heart on ventral side; runs obliquely dorsocranially, collecting from ventral, left, and dorsal surfaces of left ventricle; enters left precava near dorsal midline of heart. Does not run for any part of course in interventricular sulcus. Right cardiac vein arises on ventral surface of right ventricle near interventricular sulcus; runs obliquely to right and curves dorsally, receiving branches from ventral and right surfaces of heart; enters left precava near right atrium. In *Neotoma*, *Rattus*, *Aplodontia*, and the squirrels the cardiac veins are similar to those in pocket gophers.

*Inferior vena cava*.—Collects blood from parts of body caudal to the diaphragm. Receives venous branches from diaphragm, liver, kidneys, body wall, pelvis, and pelvic limbs.

*Common iliac vein*.—The veins of the pelvic extremity, with one exception, are venae comites, and have the same courses as the arteries. There is usually only a single vein with each artery, but there may be two vessels. The fact that a vein unaccompanied by an artery is a rarity in pocket gophers, and to a lesser degree in the cat (cf. Reighard and Jennings, 1930), suggests that the main superficial veins, so highly developed in man, are persistent anastomoses of venae comites of superficial arteries, the latter vessels having disappeared.

*Lateral superficial vein*.—Not accompanied by an artery. Begins on dorsal venous arch of foot; crosses peroneal muscles and gastrocnemius; runs proximad on surface of *M. biceps femoris*. Anastomoses with popliteal vein just above knee; passes between *Mm. femoroccygeus* and *biceps femoris* near hip joint; empties into inferior gluteal vein.

Branches of common iliac vein are similar to branches of the artery of that name. The two iliaes unite to form the vena cava inferior, dorsocaudal to division of dorsal aorta. Near kidneys, postcava becomes more ventral; lies to right of midline. Receives branches in abdominal cavity which correspond to branches of abdominal aorta, courses of which have been described. Near level where ilio-lumbar veins enter, in females, postcava receives two ovarian veins; in males, the right spermatic. Large renal veins each receive a supra-renal vein. In males, left renal vein receives minute left internal spermatic vein. Postcava passes to liver; there joined by several hepatic veins. As it emerges from liver, two large phrenic veins enter from right and left halves of diaphragm. Inferior vena cava then runs to right atrium.

*Vena portae* (fig. 25).—Collects blood from the abdominal segment of the alimentary tube, including the pelvic rectum, and ends by branching into the liver. Formed by union of superior mesenteric and splenic veins near the pyloric constriction.

*Superior mesenteric vein*.—Begins on surface of caecum as ileocaecocolic vein, receiving tributaries from caecum, colon, and ileum similar to branches of ileocaecocolic artery. Middle paracaecal vein, however, occasionally absent in *Thomomys*. After leaving caecum, superior mesenteric runs in intestinal mesentery, receiving intestinal branches from jejunum-ileum. Opposite beginning of right colic loop, cranial paracaecal and right colic veins unite with superior mesenteric; these may join to form short common vessel before emptying into mesenteric vein, or may enter separately. In mesoduodenum, superior mesenteric receives inferior pancreaticoduodenal vein from duodenum and pancreas, with branches similar to those of artery, and unites with splenic to form portal.

Splenic vein in pocket gophers receives coronary vein from stomach and inferior mesenteric vein from small intestine. Union of inferior mesenteric with splenic is regularly the condition in man, as in pocket gophers, but I do not know of other mammals in which that is true. Probably this feature is a result of the approximation of colon and stomach.

*Inferior mesenteric vein*.—Commences in pelvis as two middle hemorrhoidal veins on lateral surfaces of rectum just cranial to anal sphincter. Accompany middle hemorrhoidal arteries and, like them, do not connect with hypogastric vessels. Near beginning of pelvic rectum, two veins unite to form superior hemorrhoidal vein. Runs for short distance on dorsal surface of rectum and then passes into the mesocolon as inferior mesenteric vein. Receives several branches from descending colon and left colic loop. Dorsal to stomach, inferior mesenteric receives middle colic vein from transverse colon and part of right colic loop; then unites with splenic vein.

*Splenic vein*.—Formed by union of several splenic branches, small veins from the part of pancreas in greater omentum and mesocolon, and short gastric veins from cardiac end of stomach. Coronary vein, draining lesser curvature and dorsal and ventral sides of stomach, enters splenic near its termination in portal vein.

*Gastroduodenal vein*.—Portal receives gastroduodenal vein before entering liver. Branches of this correspond closely with those of gastroduodenal artery which has been described. Drains superior part of duodenum, associated pancreatic tissue, pylorus, and greater curvature of stomach.

Portal vein accompanies hepatic artery and bile duct to liver. Near porta hepatis, divides into three branches: small branch enters caudate lobe; larger branch passes to left lateral lobe; another about same level to right lateral lobe. These give branches to right and left central lobes. Various terminal branches of portal vein break up into capillaries in liver tissue. These unite again to form hepatic veins which empty into the postcava.

## UROGENITAL SYSTEM

The urogenital system was investigated in specimens of both sexes in *Thomomys bottae*, *Thomomys bulbivorus*, and *Geomys bursarius*. Several features of importance were also examined in specimens of *Sciurus griseus*, *Citellus richardsoni*, and *Apodontia rufa*.

### EXCRETORY ORGANS

*Kidney*.—Left kidney dorsal to stomach; right kidney covered ventrally by caudate lobe of liver, more cranial in position than the left. Latter depressed on ventrocranial surface because of its relation to stomach; right kidney retains its shape and makes a deep impression in liver. Both are normally reniform. Internally, a single pyramid as in many mammals; long, nipple-like papilla projects into large pelvis.

*Suprarenal bodies*.—Not part of the urogenital system, these glands of internal secretion are mentioned here because of their topographical relations to the kidneys. Small, irregular, lying in contact with craniomedial surfaces of kidneys. Internally similar in structure to those in other mammals.

*Ureter*.—Leaves kidney at hilus; runs caudad under peritoneum to fundus of bladder; passes dorsally over ends of genital ducts as usual.

*Bladder*.—Relatively small. Pocket gophers rarely drink; the amount of water lost in urine is not large. If the food is dry a captive animal will drink water; the same, if it is exposed to heat. But under normal conditions an animal may live a year or more without drinking. Ventral ligament of bladder extensive; lateral ligaments, in which ureters run, small; urachus obsolete. Vestiges of umbilical arteries distinguishable in ventral ligament in some specimens, but not in others. In male specimens, rectovesical pouch large, as is recto-uterine pouch in females.

### MALE GENITAL ORGANS

*Testis*.—Adult testis fluctuates considerably in size; length, 9 to 20 mm. and width, 6 to 12 mm. Testes of immature males hardly half as large as those of adults in quiescent condition. With seasonal increase in bulk of testis, a comparable increase in vascular supply. Testis covered by hard, dense *tunica albuginea*, by peritoneum and fascia; but, since scrotum incomplete and temporary, vaginal sac lacking as such. Seminiferous tubules may be seen through coverings of testis during breeding season.

*Epididymis*.—Undergoes cyclic changes during breeding season. Caput much smaller than cauda, corpus narrow, cauda long and pendant-like. Epididymis consists of much coiled tube of fine diameter (some 0.25 mm.). Fat body attached to epididymis and laterodorsal to it; varies in size with the season; reaches considerable size during quiescent period, before breeding season, but reduced during and after this period. Nutrient is doubtless stored in this to tide over the stresses of the reproductive season.

*Ductus deferens*.—Emerges from cranial end of cauda epididymis; runs short distance between this and urethra, looping around ureters as usual in mammals.

*Ligaments*.—Testis and its ducts are supported by several short mesenteries: the mesorchium and gubernaculum. The former represents the mesentery of the gonad proper, together with that of the ductus deferens. Ligament of gonad is narrow, between testis and epididymis, whereas mesentery of ductus deferens is larger; suspends testis, epididymis, and duct from dorsolateral body wall. Gubernaculum attaches solidly to both testis and epididymis, a well-marked structure in adults. Attaches by opposite end to fascia of caudal end of scrotum.

*Scrotum*.—Poorly developed in pocket gophers, but in the breeding season the testes pass through large inguinal canals and form swellings on either side of the penis and anus. The cauda epididymis remains outside the abdominal cavity longer than the rest, and may be palpated in animals outside of the breeding season. The caput epididymis, however, was not found in the scrotal pouch in any specimens examined. Skin surrounding the cauda during the breeding season wrinkled, relatively hairless. Possibly the sperm have reached a stage of maturity by the time they reach the cauda epididymis in which a lower, controlled temperature is required, and this may be not so necessary in the rest of the male reproductive tract.

Cremaster muscle, covering scrotal sacs externally, moderately well developed. Longitudinal fibers of *M. cutaneus maximus* pass over scrotal swellings and probably aid in support and ascent of testis.

*Ejaculatory ducts*.—Ducti deferentia pass dorsal to bladder without exhibiting any enlargement comparable to ampullae; joined by ducts of seminal vesicles, or glands, to form ejaculatory ducts. These much narrower than deferential ducts, which condition seems chiefly caused by a reduction of the muscular coat. Approximately 4 mm. long; lie close together; enter urethra by two irregular, slitlike openings.

*Seminal vesicles* (more properly, glands).—Consist of main, medial, tubular lobe, bent ventrally at cephalic end, and one (or several) smaller, club-shaped lobes lateral to this. May be larger on one side than on other. During breeding season elongate considerably; in fresh specimens translucent. Seminal gland opens by small pore on dorsolateral side of ejaculatory duct.

*Prostate*.—No specialized coagulating gland as in certain other rodents. Prostate a paired structure, almost surrounding neck of bladder and beginning of urethra. Lobes do not meet dorsally or ventrally, and muscle of membranous urethra extends as far cranial as entrance of ejaculatory ducts. In sexually active animals, prostate gland resembles two bunches of grapes; lobules club-shaped, narrow ends converging to open by several ducts into sides of urethra near openings of ejaculatory ducts.

*Utriculus prostaticus*.—A minute depression in the middorsal line of the urethra, about 2 mm. caudal to the openings of the ejaculatory ducts, appears to be the utriculus.

*Bulbo-urethral glands*.—Small compact bodies lying mediocranial to crura penis and lateral to *M. rectocavernosus*. Visible without much dissection after removal of skin. Rounded, with tendency to be bilobed. Duct runs cranioventrad; enters dorsolateral sides of membranous urethra at base of penis. During breeding season these glands about double their quiescent dimensions.

*Urethra*.—Extends from base of bladder to orifice at distal end of penis. Runs dorso-caudad between lobes of prostate; receives ejaculatory ducts and those of prostate; increases in size; from this point to penis surrounded by *M. sphincter urethrae membranaceae*. Continues caudad; passes dorsally over symphysis pubis; enters penis. In penis, urethra surrounded by bulbocavernosus muscle and erectile tissue of corpus cavernosus urethrae. Orifice several millimeters (2 to 4) behind tip of glans. Ventral (that is, urethral) margin of orifice forms bilobed foliate papilla; on urethral side of this papilla a depressed area. Opening of urethra transversely slitlike and puckered.

*Penis*.—Two parts, as characteristic of rodents, of approximately equal lengths; in normal resting position form obtuse angle with each other. Distal segment in this position directed nearly as much ventrad as caudad, a condition which Tullberg (1899) considered to be characteristic of fossorial rodents. Penis short; in *Thomomys talpivorus* some 18 mm.

(when straightened) from symphysis pubis to extremity. In much smaller *Thomomys douglasii*, however, noticeably longer than this. Distal joint contains tapering os priapi (baculum), which projects into long papilla centralis.

Penis consists of usual three corpora cavernosa; two corpora cavernosa penis, and corpus cavernosus urethrae. Latter poorly developed, loosely connected to other two bodies. Crura penis, consisting of proximal ends of corpora cavernosa penis, solidly attached to medial sides of hip bones, between ventral ischial tuberosities and roots of the symphysis. Oval scars mark places of attachment on bones. M. ischioavernosus surrounds each crus on all save ventromedial side; fibers run longitudinally; arise from hip bone; insert on dense fascia of crus. Ligament connects base of narrow symphyseal bar to ventrolateral surface of each crus penis.

Corpora cavernosa penis lie close together; rounded in cross section; separated at proximal end of penis by wide septum, each enclosed in dense connective tissue sheath. Septum incomplete near joint between distal and proximal parts of penis. Wide groove on ventral side of approximated corpora cavernosa penis contains more spongy corpus cavernosus urethrae and urethra, erectile tissue of former without definite sheath. At base of penis, during breeding season, corpus urethrae exhibits a bulbar expansion.

Proximal end of penis bone swollen; crowds out cavernous bodies dorsal and lateral to it. Cavernous body of urethra increases in size distal to this enlargement, coming to surround os priapi in naked glans penis. The glans penis is thus similar morphologically to that in man, although the homology has been denied for some rodents.

Glans highly vascular and erectile; relaxed it is wrinkled, irregular. The different species show some variation in the appearance of this organ, but not to the same degree as is shown in the Muridae (Bittera, 1918), in the Sciuridae (Pocock, 1923), or in the Dipodidae (Mehely, 1913; Vinogradov, 1925).

In *Thomomys bulbiivorus*, glans some 8.5 mm. long; about 3.5 mm. represents length of fingerlike papilla centralis. Tip blunt, covered with delicate skin. A few longitudinal wrinkles around base of papilla centralis most noticeable on dorsal side. On each side of proximal two-thirds of papilla there are regular rows of delicate, short, recurved spines, about eighteen on each side. Papilla lingualis (Tullberg, 1890) bilobate, each lobe gutterlike. Proximal to papillae, a ring fold, regularly scalloped, incomplete dorsally. A fold of skin connects the ring fold and the papilla lingualis ventrally, and on either side of this there is a small lateral papilla. The glans proximal to these structures is irregularly wrinkled and exhibits minute papillae on its surface.

In *Geomys bursarius*, glans penis longer than in *Thomomys*, more cylindrical, with numerous small papillae on its sides. Papilla centralis shorter, somewhat conical, bent slightly dorsad at its tip; papilla lingualis larger, deeply cleft, with ventrally directed flaps on medial and lateral sides of each lobe; ring fold high, regularly scalloped; papilla centralis with more numerous spines on sides and dorsal surface.

Os priapi symmetrical. Proximal end enlarged and rounded; bone tapers from this to a blunt point. In *Thomomys douglasii* and *Thomomys monticola* it is much larger than in the other forms.

Pair of preputial glands present in penis. Prepuce wrinkled, inner surface delicate. A fringe of stiff hairs surrounds preputial opening. The penis is normally retracted completely; indeed, the external male genitalia, except during the breeding season, are much like the female organs.

The penis in pocket gophers exhibits characters similar to those of the muroid rodents but none of the specializations of the squirrels. The simple, symmetrical os priapi, the papilla lingualis, the ring fold, the small spines, and the preputial glands all agree with conditions in the muroids.

## FEMALE GENITAL ORGANS

*Ovary*.—Lies in abdominal cavity, unlike that in rat and mouse (Robinson, 1887) which lies in a special peritoneal sac, separated from the rest of the body cavity. Ovoid in shape, small, about the size of a grain of rice in the adult. Lies caudal to the ostium, in contact with coiled uterine tube. Previous to ovulation, blisterlike follicles are visible to the naked eye.

*Uterine tube*.—Ostium abdominale opens into peritoneal cavity toward midline, cranial to ovary. Fimbriae extremely complicated, much as in the rat. Uterine tube regularly coiled forming a cycloid figure (with tracing point produced); peritoneal covering fused so that it must be dissected away to straighten the tube. Ostial end more simply arranged, makes approximately a right angle with rest of tube. In *Thomomys bottae*, uterine tube, in normal position, measures 15 mm.; slightly larger in the other two species of pocket gophers examined. Coiled uterine tube passes into muscular wall of uterus, one incomplete coil being made in this wall before tube opens by ostium uterinum.

*Uterus*.—Of duplex type characteristic of rodents, although there is a body which externally gives no evidence of division. Internally, however, body completely divided; two parts open separately into vagina. Walls of uterus, both horns and body, thrown into folds; thick and muscular. Blastodermic vesicles become implanted in horns of uterus.

*Vagina*.—Undergoes changes in size during the breeding season. At this time and for a while after parturition, lumen greater than during quiescence. Walls of vagina thinner than those of uterus. As in the muroids, no urogenital sinus in female pocket gophers, vagina opening to exterior independently from urethra. Vulva elongate transversely and, as in the muroid rodents (Miller, 1895), closed by a delicate membrane except during the breeding season.

*Ligaments*.—Uterine tubes, uterine horns, and about half of body of uterus are peritoneal, suspended on each side by a large mesentery which represents the broad ligament. A deep recto-uterine pouch between the rectum and the uterus and vagina. Most cephalic part of the broad ligament, the diaphragmatic ligament, thickened and folded over on itself, attaches to dorsal body wall near cranial end of kidney. Mesovarium, uniting ovary to uterine tube, short but quite distinct. Round ligament present in pocket gophers, but poorly developed—little more than an oblique peritoneal ridge on the broad ligament, attaching to dorsolateral wall of pelvis. Here almost continuous with lateral ligament of bladder.

*Urethra*.—The female urethra is similar to that of the male, except that it has no connection with the reproductive tract. Lies for most of its length on ventral walls of uterine body and vagina. Near vulva it runs ventrad in clitoral eminence, opening inside the prepuce.

*Clitoris*.—Similar to penis of the male, except that there is no corpus cavernosus urethrae or os priapi; the other structures, while present, are rudimentary. Glans clitoridis papilla-like, situated ventrocranially to opening of urethra. Corpora cavernosa clitoridis small but distinct; composed of erectile tissue. Preputium clitoridis completely surrounds glans and urethral orifice. Opening of the prepuce longitudinally slitlike. Preputial glands, similar to those of the male, but smaller, are present. Clitoral eminence contains a large amount of fatty tissue.

This type of clitoris has been called "phallus canalisatus" by Henneberg (1917). It is found in some lemurs and some insectivores, and it is present in the muroid and bathyergoid rodents. Apparently the ventral halves of the labia minora have closed behind the urethral orifice, somewhat as similar structures do in male mammals, separating the urethral and vaginal openings.

The female external genitalia are precisely like those structures in the muroid rodents. In both the genera of squirrels and in *Aplodontia* there is a short urogenital sinus and the glans clitoridis is contained within it. Characters of the genitalia have been considered of phylogenetic importance, and consequently the great similarity in both male and female genitalia between the geomyoid and muroid forms argues for the near relationships of these rodents.

## CONCLUSIONS

The results of this anatomical investigation of the pocket gopher may be divided into conclusions relating to morphological problems, and those concerned with the relationships of this rodent.

The morphological conclusions are (1) those which relate primarily to rodents and (2) those which relate to mammals as a Class. The first group consists of the following:

The primitive number of ribs in rodents (other than hystricomorph) is probably thirteen rather than twelve; the frequent occurrence of the former number in pocket gophers is probably atavistic. The falciform bone is constantly present in the manus.

*M. cleido-occipitalis* is typically discrete. *M. scalenus anterior* is usually absent. There are no epaxial muscle elements in the scalenus complex of most rodents; *M. levator scapulae* separates *M. scalenus* from the epaxial muscles. *M. sartorius* is absent in many rodents, but it is present in the *Sciuridae*. *Mm. adductores femoris* of rodents may be homologized with those of man by considering the relations of these muscles to the branches of the obturator nerve. The union of the tendons of *M. flexor digitorum tibialis* and *M. flexor digitorum fibularis* is not necessarily indicative of hystricoid affinities, as stated by Dobson (1882), but is a primitive character independently retained by several muroid forms and by the geomyoid rodents.

The unusual relationship of the external jugular vein of muroid and geomyoid rodents is probably the result of an anastomosis between the cephalic and true external jugular veins, ventral to the clavicle. A condition much like this hypothetical intermediate stage is present in *Aplodontia* and *Citellus*. The internal jugular vein is usually vestigial, and the brain is drained chiefly by the postglenoid or by the subsquamosal vein. The internal maxillary artery arises from the stapedial in most rodents; it arises from the external carotid in the pocket gopher, as in man.

The more general conclusions, relating to mammalian anatomy, are the following:

The medial tarsal bone is probably not a sesamoid.

Insertions of muscles are usually much more constant in location than are origins. In the adductor muscles of the thigh, however, the origins are more constant than the insertions.

Muscles tend to retain their topographical relations to nerves; these relations are important evidences for, or against, homologizing mammalian muscles with those in man or in other mammals.

When a muscle passes over a bone on its way to its insertion, and if no change of function is involved, the origin may shift to this bone. This is true, for example, in *M. femorococcygeus* and *M. caudofemoralis*.

When the contracting function of the whole or part of a muscle becomes unimportant, the muscle (or its part) frequently becomes a ligament. Examples of this are found in *M. coccygeus*, *M. femorococcygeus*, and *M. abductor ossis metatarsi quinti*.

When a muscle in its evolution comes to occupy a more proximal position than the primitive one, the nerve which supplies the muscle tends to arise nearer the roots of the plexus. Examples of this are to be found in *M. piriformis*, *M. subclavius*, and *M. psoas major*. On the contrary, when a muscle becomes situated more distally than before, the nerve supplying it is a more distal branch. Examples of this are *M. tenuissimus*, *M. extensor digitorum brevis*, and *M. quadratus plantae*.

Although great modifications of attachment occur in the muscular system of mammals, "heritage" exerts a great influence on the muscular system. The muscles of the hind limb in *Thomomys* and *Dipodomys* are very similar in spite of the difference in manners of life.

The evidences of relationship drawn from the muscular system, while important within families, are too complex to be of much importance in more comprehensive groups.

*M. jugulohyoideus* is a primitive element of the deep facial group, lost with the reduction of the anterior horns of the hyoid in man, in pocket gophers, and in the muroid forms. *M. deltoideus* is probably, primitively single; it becomes divided in animals in which the action of abduction is not important. *M. piriformis* is apparently derived from *M. gluteus medius*, from which it may not be separate. *M. femorococcygeus* is primitively part of *M. gluteus maximus*. *M. flexor tibialis* and *M. tibialis posterior* have probably been derived from a single muscle, retaining an intimate association in the sciurormorph rodents and many other primitive mammals.

The branches of the common peroneal nerve do not always contain homologous nerve fibers.

The cephalic, basilic, and saphenous veins are apparently persisting anastomoses between the veins accompanying superficial arteries.

The relationships of the pocket gophers, as indicated anatomically, are first with the pocket mice and kangaroo rats, and secondly, less certainly, with the muroid rodents.

[Occasional reference is made to cranial foramina in discussing the phylogenetic position of the pocket gophers. This part of the investigation has been published separately (Hill, 1935b).]

The pocket mice and kangaroo rats are currently, at least by American systematists, placed in a separate family, the Heteromyidae. Coues (1875b) gives a number of differences between the two groups, all of which, however, are correlated with the different manners of life of these rodents. Other differences are the following: In heteromyids the two infraorbital foramina are connected by an opening in the nasal septum; the entepicondylar foramen is present in the humerus; the posterior angular process of the mandible is not elevated and is weak; the internal pterygoid muscle does not invade the sphenopterygoid canal; the caudal angle of the scapula is produced; and the symphysis pubis is of moderate length, rather than reduced or absent.

The following characters exhibited by both groups indicate a closer relationship between the pocket gophers and the heteromyine forms than is ex-



pressed in a classification giving family rank to both groups. These characters are individually of greater importance than those of the preceding list.

The external, fur-lined cheek pouches, with almost identical musculature; the infraorbital canal, sunken in the side of the rostrum, opening anteriorly near the premaxillo-maxillary suture; the persistent premolar; the similarities of the deciduous premolar and the unworn permanent dentition (cf. A. E. Wood, 1935); the fused and reduced anterior horns of the hyoid (Tullberg, 1899); the vestigial stapedial canal; the fissures and foramina around the tympanic bulla; the pseudostyloid process of the radius; the solidly fused tibia and fibula; the complex similarities in the muscular system; the shape and pattern of the digestive tract; and the structure of the external genitalia.

It would appear that the currently recognized family Heteromyidae should therefore be reduced to a subfamily of the family Geomyidae.

The anatomical characters that indicate the relationship of the family Geomyidae (in the broad sense) with the other families of rodents are not so unequivocal. Winge (1888) associated the Geomyidae with the Sciuridae because of the similarity of the zygomasseteric structure in the two groups. Tullberg (1899) followed Winge with somewhat less conviction, because he considered other structures as well. Miller and Gidley (1918) in reviewing the suprageneric groups of rodents, again considering almost exclusively the masseter muscle and the infraorbital foramen, placed the pocket gophers as a family in the superfamily Sciuroidea, implying that the differences between the pocket gophers and the squirrels were not of much greater significance than those between the former animals and the pocket mice.

Characters in which geomyids resemble the sciuroid rodents and differ from the muroids are:

The nasolacrimal canal begins in the orbit, not on the side of the rostrum; the lacrimal bone usually forms part of its walls. The infraorbital foramen is small; so are the incisive foramina. The auditory ossicles are shaped like these bones in the squirrels (cf. Tullberg, 1899). The anterior part of *M. masseter lateralis profundus* arises from the rostrum; *M. masseter medialis* is restricted to the zygoma and orbit in origin and does not penetrate the infraorbital foramen. The stomach is simple, without a cornified layer in the cardiac part.

Of these characters the first, second, and fifth are interdependent, and are correlated with chewing habits. While it is not reasonable to suppose that the zygomasseteric structure in pocket gophers could have been derived from that of modern muroids, its resemblance to the type characteristic of the squirrels might well be purely convergent. It is a character probably subject to the influences of natural selection, and similarities in such characters are not as important as in structures which are subject to chance variation only. The similarities shown in the lacrimal canal and in the stomach are retentions of primitive characters, and hence of less significance than secondary conditions would be. The reduction of the incisive foramina is a specialization and not evidently adaptive, but a similar reduction has occurred in many other mammals.

There are numerous similarities between the pocket gophers and the squirrels besides these, but they are also shared with the muroid rodents.

The pocket gophers and their allies resemble the muroid rodents, and differ from the sciuroids and *Aplodontia*, in the following structures:

The heads of all ribs articulate intervertebrally. The manubrium sterni is roughly T-shaped, instead of diamond-shaped. The zygomatic bone (jugal or malar) does not reach the lacrimal, nor does it enter into the mandibular fossa. The rostrum is elongate and the nasal bones relatively narrow. The alisphenoid is emarginate anteriorly; the maxillary bone forms part of the floor of the cranial cavity. The alisphenoid and sphenopterygoid canals are incomplete dorsally. The horns of the hyoid bone are greatly reduced in size; the anterior horns are vestigial and are not segmented. The tibia and fibula are fused; there is a common proximal epiphysis for the lower leg bone.

*M. jugulohyoideus* is absent. *M. caudofemoralis* is simple; it inserts on the medial epicondyle; in the squirrels it is partly double, one part inserting on the caudal surface of the femur. *M. femorococcygeus* inserts chiefly on the patella; it is distinct from *M. gluteus maximus*. The tendon of *M. peroneus longus* is separated from those of the other peroneal muscles; it runs in a special groove on the lateral malleolus. The tendon of *M. tibialis posterior* runs in a sheath and groove on the medial malleolus, separated from those of *M. flexor tibialis*.

The tongue exhibits only a single vallate papilla. The left lung is single. The pericardium is in contact with the ventral body wall. The external jugular vein emerges caudal to the clavicle and lies ventral, that is, superficial, to that bone.

The glans penis is symmetrical; it exhibits a ring fold, a papilla lingualis, and is partly covered with spines. There are preputial glands. The female urethra opens in the clitoral eminence; there is no urogenital sinus. The glans clitoridis is small, papilla-like, and symmetrical. It is situated in the clitoral eminence cranial to the vaginal orifice.

Most of these characters are specializations; they are found in animals adapted to very divergent habits of life; and they are characters which have no evident adaptive significance. Consequently they are more important than the similarities between the pocket gophers and the squirrels.

There are, however, differences between the Geomyidae and the Muroidea which militate against the too close association of these groups. These characters are those which have been listed in connection with the resemblances between the pocket gophers and the pocket mice. The similarities between the Geomyidae and Sciuridae that have been mentioned, and which have been considered highly significant by previous authors, lend weight to this. I consider the differences between the Geomyidae and the Muroidea to be important enough to give the former group superfamily status. The Geomyoidea may then be placed with the Muroidea in the Myomorpha. The Myomorpha may be characterized thus: Zygomatic bone (jugal) reduced, separated from lacrimal by maxillary and from mandibular fossa by squamosal (except in the Dipo-

doidea) ; rostrum and palate narrow ; alisphenoid emarginate, exposing maxillary bone in floor of cranial cavity ; petrotympanic separated from the alisphenoid by a fissure ; anterior horns of hyoid vestigial, unsegmented ; cheek teeth  $\frac{1}{4}$  or less ; tibia and fibula fused ; tongue with single papilla vallata ; left lung single ; preputial glands present ; female urethra completely separate from vagina, opening in clitoral eminence ; glans penis with spines, symmetrical.

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THE PTERYLOSIS OF THE FALCONIFORMES  
WITH SPECIAL ATTENTION TO THE  
TAXONOMIC POSITION OF THE OSPREY

BY

LAWRENCE V. COMPTON

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# THE PTERYLOSIS OF THE FALCONIFORMES WITH SPECIAL ATTENTION TO THE TAXONOMIC POSITION OF THE OSPREY

BY  
LAWRENCE V. COMPTON

(Contribution from the University of California Museum of Vertebrate Zoology)

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## INTRODUCTION

THE PRESENT STUDY of the pterylosis of the Falconiformes is the outgrowth of a project that had for its purpose the investigation of the adaptive modifications of the osprey (*Pandion haliaetus*). The pterylosis was one of the first features investigated, and a comparison of the feather tracts of the osprey with those of the hawks with which this species is customarily grouped showed that not all of the many differences between them could be explained on the basis of adaptive modification alone. This suggested that similarities might be found among other forms and that the taxonomic position of the osprey was not well established.

The literature reveals that the questionable taxonomic position of the osprey has been realized by many, but that there have been few attempts to solve the problem by a careful comparison of this species with the forms supposedly related to it. The osprey has always been considered a hawk and has been placed in the order which contained the hawks and, for many years, the owls. However, its position within this order has been subject to much shifting.

Early systematists were able to see characters in the osprey which indicated relationship to the eagles (Magillivray, 1836, p. 111; Gray, 1869, p. 15). Other authors have thought the osprey to be related to the kites. Brehm (1878, p. 668), while including the osprey in his subfamily Aquilinae, held that it might be regarded as constituting a separate subfamily, Pandioninae, a connecting link between the eagles and the kites. His "kites" constituted a somewhat indefinite group that included the present-day subfamilies Elaninae, Perninae, and Milvinae, which are commonly called kites, as well as some members of the subfamilies Buteoninae and Circinae.

Ridgway, although he at one time grouped the osprey with the kites (Milvinae), finally (1875, fn., p. 228) placed it in a separate group Pandiones under the Buteoninae.

Suschkin (1900, p. 526) also held to the theory that the osprey was related to the kites and placed *Pandion*, *Pernis*, *Baza*, *Elanoides*, and *Leptodon* in a single group. Apparently he later changed his opinion on this matter, for Pycraft (1902, p. 315) wrote: "But from views he [Suschkín] expressed in conversation, he would, I suspect, probably make a separate sub-family for *Pandion*—Pandioninae; and most, I think, will feel this advisable."

Certain osteological characters have long been used to show that the osprey is similar to the owls and that this species may represent a connecting link between the owls and the hawks. Nitzsch (1867, fn., p. 54) said: "The absence of the aftershaft causes this Falcon [the osprey] to approach the Owls as much pterylographically as it does zoologically in the reversible toe, and anatomically in the non-pneumatic femora and the completely closed osseous canal on the *os metatarsi* for the passage of the sinew of the *extensor digitorum communis*." (W. DeW. Miller [1915, p. 139] has shown that the feathers of the osprey have an aftershaft.) Milne-Edwards (1869, pp. 413, 419) also directed attention to the fact that the tarsometatarsus and tibiotarsus of the osprey have several characters in common with those of the owls.

After reiterating these points of similarity, Seebohm (1895, p. 14) added: "The *Pandionidae* also agree with the *Striges* and the *Psittaci*, but differ from the *Falconidae* and the *Gypogeranidae*, in having only the second and third digits directed permanently forwards." In his classification *Pandion* was the type of one of the three families in his suborder *Accipitres*, the other two families being *Gypogeranidae* and *Falconidae*. Somewhat comparable views have been expressed by Beddard (1898, p. 478) and Gurney (1882, p. 594). Sharpe (1891, p. 63), in a review of the various attempts at classification of birds, said: "I still maintain the correctness of my opinion that the Ospreys are not Eagles at all, but represent an intermediate group between the *Accipitres* and the *Striges*."

In writing about the similarity of certain characters of the osprey to those of the owls, Newton (1893, p. 661) stated: "... the most important parts of its internal structure, as well as its ptilosis, quite forbid a belief that there is any near alliance of the two groups." Knowlton (1909, p. 231) summed up the evidence as follows: "... all things considered, it seems likely that they [the ospreys] find their closest relatives among the Honey Buzzards and their allies, being by some authorities ... placed in the subfamily *Perninae*, but it is perhaps best to regard them as constituting by themselves a distinct subfamily (*Pandioninae*)."

The tendency to segregate *Pandion* in a section by itself began early, with the result that this genus has been the type of subfamilies, families, and suborders. Sharpe (1874, p. 448) established the suborder *Pandiones*, equivalent in rank to his suborders *Falcones* and *Striges*. He included in *Pandiones* the two genera *Pandion* and *Polioaëtus* [*Ichthyophaga*]. This inclusion of *Polioaëtus* was contested by Gurney (1878, p. 455), who showed that *Polioaëtus* is related to *Haliaeetus*.

Coues (1903, p. 698) placed *Pandion* in a separate family *Pandionidae*, under the suborder *Falcones*. He wrote of the osprey: "The structural characters are rather those of buteonine than falconine birds of prey, in the coracoid arrangement, etc."

Swann (1924, p. ii), in discussing Sharpe's suborders of the *Accipitres*, said: "The second [suborder *Pandiones*] is now recognized as forming a subdivision only of the family *Falconidae*..." In his general remarks upon the subfamilies of his family *Falconidae*, Swann (*op. cit.*, p. iii) wrote: "... there

seems no adequate reason to make a separate sub-order or even family of this bird [the osprey] on account of the reversible outer toe. . . ."

Peters (1931), in his check list of the birds of the world, placed the osprey in the subfamily Pandioninae at the end of the family Accipitridae. The latest edition of the American Ornithologists' Union Check-list (1931) presents a similar classification.

The current classification of the hawks may be outlined as follows: The order Falconiformes is divided into two suborders, the Cathartae and the Falcones. The suborder Cathartae embraces a single family, the Cathartidae, whereas the suborder Falcones is divided into three families: the Sagittariidae, Accipitridae, and Falconidae. The Sagittariidae is represented by one genus. The Accipitridae has nine subfamilies: the Elaninae, Perninae, Milvinae, Accipitrinae, Buteoninae, Aegypiinae, Circinae, Circaetinae, and Pandioninae. The Falconidae has four subfamilies: the Herpetotherinae, Polyborinae, Polihieracinae, and Falconinae.

It can easily be seen from the foregoing review that few pertinent facts concerning the morphology or taxonomic position of the osprey have been recorded. Most of the characters which have been used to classify this species have undergone so much adaptive modification that they are unreliable.

With the realization of these problems of relationship of the osprey, the study of the pterylosis became important, not so much for the investigation of its adaptive modifications as for its phylogenetic significance throughout the Falconiformes.

#### METHODS

The principal method used in preparing specimens for examination was that of clipping off the contour feathers about three-eighths of an inch from the body and plucking or clipping the down between them. In very closely feathered areas such as those on the head, plucking the feathers and making note of the pits was frequently a more satisfactory method of determining the feather arrangement.

When study skins were used, the tracts were examined by carefully parting the feathers. This method proved fairly satisfactory with the tracts of the dorsal surface, but on the ventral surface the sewed incision usually distorts the tracts so badly that little can be learned concerning them.

The drawings were made from tracings of natural-size photographs and hence accurately portray the pattern and extent of each feather tract.

#### SPECIES EXAMINED

As many species as possible were obtained as alcoholic specimens, but when these could not be procured, study skins were resorted to. In the following list the expression "alcoholic" refers to any specimen preserved in a wet condition. The classification used is that of Peters (1931). Not all the forms listed as examined are treated in the descriptions. Species and subspecies examined:

1. *Cathartes aura teter* Friedmann. Western Turkey Vulture. One alcoholic.
2. *Sagittarius serpentarius* (J. F. Miller). Secretary Bird. One skin.

3. *Elanus leucurus majusculus* Bangs and Penard. White-tailed Kite. One alcoholic.
4. *Elanoides forficatus forficatus* (Linnaeus). Swallow-tailed Kite. One skin.
5. *Ictinia mississippiensis* (Wilson). Mississippi Kite. Three alcoholics.
6. *Rostrhamus sociabilis plumbeus* Ridgway. Everglade Kite. Two skins.
7. *Haliastur indus intermedius* Blyth. Malayan Brahmany Kite. One skin.
8. *Accipiter gentilis atricapillus* (Wilson). Eastern Goshawk. One alcoholic.
9. *Accipiter cooperii* (Bonaparte). Cooper Hawk. Three alcoholics.
10. *Accipiter striatus velox* (Wilson). Sharp-shinned Hawk. Three alcoholics.
11. *Melierax metabates* subsp.? Chanting Goshawk. One skin.
12. *Buteo regalis* (G. R. Gray). Ferruginous Rough-legged Hawk. One alcoholic.
13. *Buteo jamaicensis borealis* (Gmelin). Red-tailed Hawk. Four alcoholics.
14. *Buteo swainsoni* Bonaparte. Swainson Hawk. Two alcoholics.
15. *Buteo lagopus s. johannis* (Gmelin). American Rough-legged Hawk. One alcoholic.
16. *Aquila chrysaetos canadensis* (Linnaeus). Golden Eagle. One alcoholic.
17. *Haliaeetus vocifer* subsp.? African Sea-Eagle. One skin.
18. *Haliaeetus leucocephalus washingtoniensis* (Audubon). Northern Bald Eagle. One skin.
19. *Circus cyaneus hudsonius* (Linnaeus). Marsh Hawk. Six alcoholics.
20. *Gymnogenys typicus* subsp.? African Harrier-Hawk. One skin.
21. *Terathopus ecaudatus* (Daudin). Bateleur. One skin.
22. *Spilornis cheela ricketti* W. L. Slater. Chinese Serpent Eagle. One skin.
23. *Pandion haliaetus carolinensis* (Gmelin). American Osprey. Two alcoholics.
24. *Micrastur semitorquatus naso* (Lesson). Pied Hawk. One skin.
25. *Phalcobæus albogularis* Gould. White-throated Caracara. One skin.
26. *Polyborus plancus plancus* (J. F. Miller). Caracara. One skin.
27. *Polyborus cheriway audubonii* Cassin. Audubon Caracara. One skin.
28. *Falco mexicanus* Schlegel. Prairie Falcon. One alcoholic.
29. *Falco rusticolus candicans* Gmelin. White Gyrfalcon. One skin.
30. *Falco peregrinus anatum* Bonaparte. Duck Hawk. One skin.
31. *Falco sparverius sparverius* Linnaeus. Eastern Sparrow Hawk. Three alcoholics.

#### CLASSIFICATION OF TRACTS

The classification of feather tracts used here is a slightly modified form of the one employed by Boulton (1927). His classification has been used by certain American workers, namely, Burt (1929) and A. H. Miller (1931). The prevailing European classification differs from this one chiefly in that the term "tract" usually applies to smaller areas and supplants the term "region."

The contour feathers are separated into the following eight tracts (figs. 1,

2, 8) : capital tract, spinal tract, ventral tract, caudal tract, humeral tract, alar tract, femoral tract, and crural tract. The boundaries of these tracts are, for the most part, natural, but some of them must be established arbitrarily. The subdivisions of the tracts, called the regions, are often indefinite in outline because of the fusion of two or more of these regions. The lateral tracts and regions are bilaterally symmetrical, and therefore only those of one side are described.

After a discussion of each tract and a definition of its regions, descriptions are given of the tract as it occurs in the various species. A typical representative is described in detail at the beginning of each family discussion. Since the osprey is considered in comparison with other falconiforms, the descriptions of its feather tracts are placed after those of the other families. In anticipation of the conclusions, the family Pandionidae is used. Where only one species within a genus has been described, this species is subsequently referred to by its generic name alone.

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### PTERYLOGRAPHY

#### THE CAPITAL TRACT

##### DEFINITIONS

The capital tract extends from the beak and cere to the neck and includes the dorsal, lateral, and ventral surfaces of the head. It consists of eleven areas, the frontal, coronal, occipital, superciliary, loreal, ocular, auricular, postauricular, malar, interramal, and submalar regions. Some workers in pterylography have placed the interramal and submalar regions in the ventral tract while including the malar region with the capital tract. A more natural grouping can be accomplished by the older system of including all the regions of the lower mandible (malar, interramal, and submalar) with the capital tract.

The frontal, coronal, and occipital regions are confluent and cover the top and back of the head. The frontal region extends from the cere to a point about opposite the middle of the eye. From here the coronal region extends pos-

teriorly over the crown to the occipital region, which is at the base of the head. All three of these regions extend down over the sides until delimited by the regions covering the lateral surfaces.

The superciliary region is an elongated area directly above the upper ocular apterium; it is bounded above by the frontal and coronal regions. The loreal region lies on the maxilla between the eye and the cere and is delimited above by the frontal region. Its feathers are bristle-like and have usually been referred to as "loral bristles."

In the falconiforms the rictal bristles are hardly distinguishable from similar bristles in the feather areas immediately surrounding them. For this reason I consider it best not to refer to a definite area as the rictal region, but to include the bristles of the maxilla with the loreal region, and those of the lower mandible with the malar region.

Above and below the eye are the ocular apteria. The upper ocular apterium lies partly on the upper eyelid and partly on the crown. It is especially well developed in the forms having a large orbital process of the lacrimal bone and in these forms is directly over this process. The enlargement of this apterium can be correlated with the increase in pressure upon the skin from beneath by the orbital process. This principle, that pressure from beneath is the cause of certain apteria, was demonstrated by Burt (1929, p. 434). The lower ocular apterium covers the lower eyelid. These two apteria are sometimes joined at the corners of the eye. The upper apterium is usually without down feathers whereas the lower ordinarily has a scattering of them. The ocular region includes the rows of eyelashes about the orbit and such feathers as may occur on the upper and lower lids.

The auricular region is a more or less pear-shaped area extending posteriorly from the corner of the mouth; it is a narrow area ventral to the eye, but enlarges posteriorly and surrounds the external auditory meatus. At its posterodorsal margin it blends with the coronal and occipital regions. The postauricular region is posterior to the malar and auricular regions, and between the occipital and submalar regions. It extends a short distance to the base of the head.

The malar region lies on the lateral surface of the ramus between the horny beak and a point below the auditory meatus. The interramal and submalar regions lie on the ventral surface between the two rami. The interramal region extends from the symphysis to a point below the orbit; from this point the submalar continues and constitutes the remainder of the throat area. At its posterior margin the submalar fuses with the postauricular and ventral-cervical regions. The submalar apterium lies directly over the ventral edge of the ramus and, when present, separates the malar from the interramal region.

#### ACCIPITRIDAE

Buteoninae. *Buteo jamaciensis borealis*.—Except for the paired submalar and ocular apteria, the entire head is closely covered with feathers. The feathers of the frontal, coronal, and occipital regions are much alike, but are heavier in the median portions of the frontal and coronal regions than in the lateral portions. The feathers of the occipital region are uniform in size and are similar to those of the median portion of the coronal region.

The loreal region is a dense mass of bristle-tipped feathers which stand out from the skin and are arranged in a definite whorl. Long, thin bristles extend downward over the tomium, and anteriorly and upward over the cere, with a few forming a thin covering for the naris.

The superciliary region consists of four or five rows of fine, bristle-tipped feathers. There is a wide upper ocular apterium which is entirely lacking in down feathers. In the ocular region four or five rows of bristle-tipped feathers occur along the orbital edge of the upper eyelid, with an additional one or two rows of scattered, less modified feathers along the lower edge of the upper ocular apterium. Along the orbital margin of the lower lid there are three to four rows of similar bristle-like feathers. A scattering of fine down feathers occurs over the surface of the lower lid.

The auricular region is narrow beneath the eye but gradually widens as it extends posteriorly. The whole region is rather closely set with feathers; the most anterior are bristle tipped, but the rest are the usual type of ear coverts. Two or three rows of stiff feathers surround the meatus. The feathers of the postauricular region have smaller shafts and are spaced farther apart than those in the auricular region; they are similar to the feathers of the occipital region. The malar region is closely feathered, especially in its anterior portion. Along the margin of the beak the feathers are modified into long, thin bristles that extend over the tomium.

The submalar apterium lies over the ventral margin of the mandible and extends from the horny beak to a point opposite the posterior corner of the eye, separating the malar from the interramal region. The interramal region extends from the symphysis almost to the end of the submalar apterium. The feathers of the first three or four rows at the symphysis are bristle tipped and project anteriorly over the beak. At its posterior margin this region fuses with the submalar region, which swings upward to join the postauricular region. Slightly posterior to the angle of the lower mandible the lateral-cervical apteria swing sharply toward the median line and constrict the ventral-cervical region.

*Elaninae. Elanus leucurus majusculus.*—This tract is essentially like that of *Buteo*. The loreal region is more elongate; the bristles are finer and fewer of them extend over the cere. The rectal bristles of the ramal region are exceptionally fine. The submalar apterium is longer and extends almost the length of the mandible.

*Milvinae. Ictinia mississippiensis.*—This tract is in general the same as in *Buteo*. In the loreal region the feathers are fewer and more bristle-like; few of them extend over the cere and tomium. There appears to be a tendency toward the development of a postmalar apterium as in *Circus*.

*Accipitrinae. Accipiter cooperii.*—The feathering of this tract closely resembles that of *Buteo*.

*Circinae. Circus cyaneus hudsonius.*—The frontal, coronal, occipital, and superciliary regions resemble those of *Buteo*. The loreal region is more elongate and the feathers of its anterior portion are much longer and provide a denser covering to the naris. These feathers extend upward from each side and nearly meet above the cere.

The most unusual feature of the capital tract in *Circus* is the presence of a facial ruff. This ruff extends posteriorly from the center of the throat (interramal region) around the angle of the mandible and posterior margin of the meatus and terminates above and behind the ear. It is composed of six to eight rows of small, stiff, closely inserted feathers, supported on a vertical ridge or fold of skin. The ruff modifies the regions through which it

Along the lower margin of the auricular region, extending from the gape to the meatus, there is an elongate area of four or five rows of stiff, highly modified feathers. This area divides at the meatus, sending a single row along the ventral margin, and a branch which gradually diminishes from five to two rows, along the anterior margin. Along the posterior margin of the meatus run the six to eight rows of the facial ruff. The rest of the auricular region below and posterior to the eye consists of small-shafted, less modified feathers.

The upper ocular apterium is relatively small. Posterior to the eye, and above and anterior to the meatus, is a small, ovoid, temporal apterium.



The malar region covers only the anterior two-thirds of the mandible; posteriorly it is supplanted by the postmalar apterium. This apterium extends to a point opposite the meatus and is bounded above by the auricular region and below by the facial ruff. The malar region is densely feathered; the feathers along the tomium and beak are bristle tipped.

The submalar apterium extends the length of the malar region and separates this region from the interramal region. The facial ruff forms the lateral portions of the submalar region and continues along the anterior edge of the postauricular region. The feathers of the ruff are stiff and closely set, whereas in the portion of the submalar region between the right and left branches of the ruff they are small and scattered.

#### FALCONIDAE

*Falco mexicanus*.—Except for the ocular and submalar apteria, the entire head is closely covered with feathers. The regions in general are more densely feathered than in *Buteo*. The frontal, coronal, and occipital regions are similar to those in *Buteo*, but the feathers of the loreal region are more closely set and less bristle-like. The tendency for these bristles to be arranged in a whorl is not so evident, since most of them project posteriorly. Only a few short bristles extend over the cere and none reaches over the naris. The superciliary region consists of six or seven rows of small feathers.

The upper ocular apterium extends the length of the eye and around its corners into the lower ocular apterium. In the ocular region there are one to three rows along the orbital edge of the upper lid, two rows along the orbital edge of the lower lid, and a few scattered down feathers on the lower ocular apterium.

The feathers of the anterior portion of the auricular region are short and closely set but become longer and farther apart as the region widens and extends toward the ear. There are two rows surrounding the meatus, but there are fewer feathers in these rows than in *Buteo*. The postauricular region is a mass of closely set feathers.

The malar region is closely feathered; few of the feathers are bristle tipped. The submalar apterium extends about the same distance as it does in *Buteo*. The interramal and submalar regions are continuous over the lower surface of the jaw. The lateral-cervical apteria cut into the submalar and cervical regions in a fashion similar to that in *Buteo*, and the posterior portion of the submalar region extends upward to meet the postauricular region.

#### CATHARTIDAE

*Cathartes aura lutea*.—There are no plumaceous feathers on the head, but it is covered with fine, highly modified, hairlike feathers. The skin of the head is heavily wrinkled and as a result little can be determined of the pterylosis, but it can be seen that all the regions are confluent.

The bristle feathers of the frontal and coronal regions are shorter than those of the occipital region. The loreal region is the most heavily feathered of the head and has most of its bristles in its upper half. These loreal bristles stand almost perpendicular to the body, most of them extending dorsoanteriorly. The feathers of the superciliary region are shorter than those of any other region and project only one or two millimeters from the skin.

The upper ocular apterium is narrow and connects, around the posterior corner of the eye, with the lower ocular apterium. There is a single row of eyelashes along the posterior two-thirds of the upper eyelid and two rows of eyelashes along the orbital margin of the lower lid. There is no down on the lower lid.

The feathers of that part of the auricular region which is beneath the eye are closely inserted and fairly long, but they become fewer and shorter in the posterior portion of this region. Two or three rows of bristles surround the meatus. The postauricular region blends with the occipital region and has feathers of a similar nature.

There is no submalar apterium, and therefore the regions on the mandible are confluent. An area between the rami, extending from the symphysis to a point directly beneath the posterior margins of the nares, is unfeathered and I propose for it the name interramal apterium.

## PANDIONIDAE

*Pandion haliaetus carolinensis* (fig. 1).—The entire head is covered with closely inserted feathers. All the regions are confluent and for the most part can be distinguished only by their relative positions, by the direction in which the feathers extend, or by the nature of the feathers.

The feathers of the frontal and occipital regions are stiffer and have heavier shafts than those of the coronal region, and in the two regions first named the feathers of the median portion are heavier than those of the lateral portions.

In the loreal region the feathers stand out from the skin and either are fine bristles or are bristle tipped. When compared to those in *Buteo*, these bristles are seen to be relatively

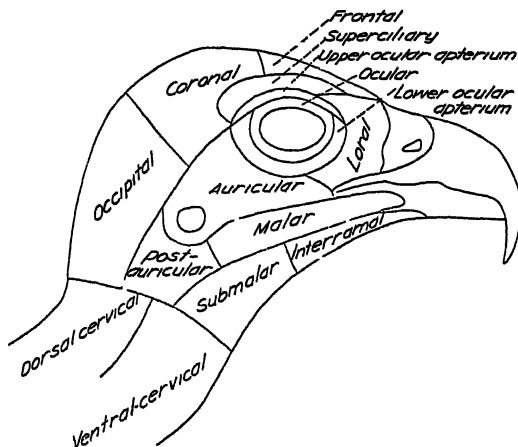


Fig. 1. Diagrammatic drawing of the head and upper neck of *Pandion haliaetus carolinensis* showing areas covered by regions of the capital tract. The dorsal-cervical and ventral-cervical regions are divisions of the spinal tract and ventral tract, respectively.

short and rather sparse, and their whorled arrangement to be less pronounced. A few of the loreal bristles extend over the edge of the cere, but none reaches the naris. The superciliary region consists of four or five rows of feathers that are smaller and of finer structure than those of the frontal and coronal regions which lie above it. There is no orbital process of the lacrimal bone in the osprey and as a result the upper ocular apterium is exceptionally narrow. Tiny down feathers are scattered over both ocular apteria. Besides the down feathers of the apteria, the ocular region consists of two rows of small feathers along the orbital edge of the upper eyelid and four or five rows of similar feathers along the orbital edge of the lower lid. The feathers of the inner row around the lids are bristles, and those of the other rows are more or less bristle tipped.

The narrow anterior portion of the auricular region consists of small feathers, the more anterior of which are bristle tipped; but as the region enlarges posteriorly the feathers become larger. Two or three rows of feathers encircle the meatus. The postauricular region is distinguished from the auricular by having fewer and somewhat finer feathers.

In the malar region the feathers of the first two or three rows lying next to the tomium and beak are bristles or are bristle tipped. The few that extend over the tomium constitute the lower rictal bristles. In the rest of the malar region the feathers are small, closely set, and normal. There being no submalar apterium, the malar and interramal regions fuse with each other.

The feathers of the first few rows in the interramal region are bristle-like and project over the beak; those of the rest of the region are normal and increase slightly in size of shaft

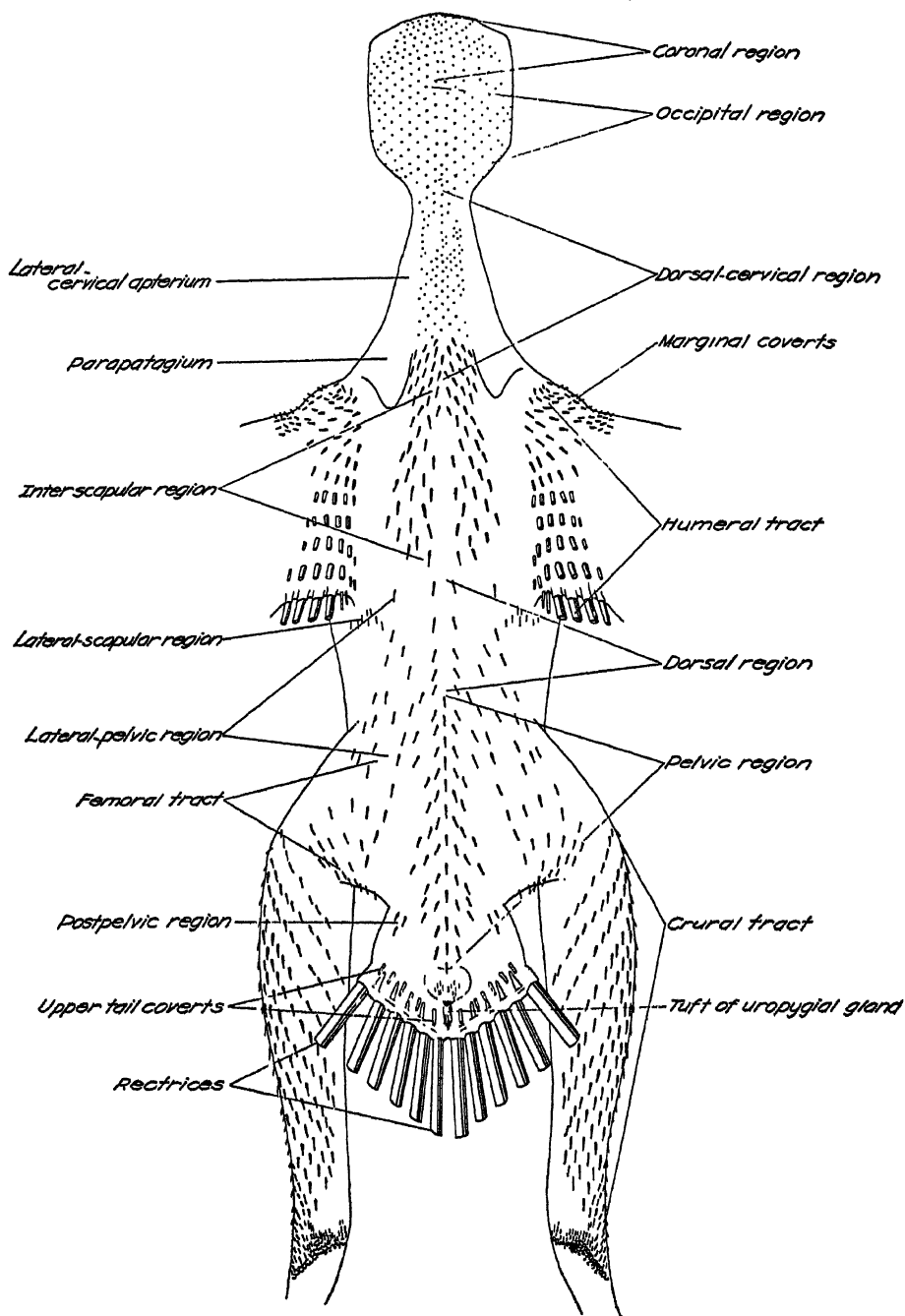


Fig. 2. Tracts and regions of dorsal surface of *Buteo jamaicensis borealis*.

as the region progresses posteriorly. The feathers of the submalar region are like those of the interramal region. Following the contour of the throat, the interramal and submalar regions gradually become wider as they extend posteriorly.

## THE SPINAL TRACT

### DEFINITIONS

The spinal tract extends from the base of the head to the uropygial gland. It consists of six regions, the dorsal-cervical, interscapular, lateral-scapular, dorsal, pelvic, and lateral-pelvic. The dorsal-cervical region extends from the base of the head to the trunk, where it divides to form the two branches of the interscapular region, each of which extends the length of the scapula. This region is characterized by heavy development of the shafts of the feathers. The dorsal region forms a short and much lighter continuation of the tract and consists of one or more rows, on each side of the median line, that extend approximately to the anterior border of the sacrum. The pelvic region is the posterior continuation of the tract and extends from the dorsal region to the base of the tail. It appears in three different patterns, (1) two wide branches, one on each side of the median line, (2) a wide tract on each side of the median line with a single row upon the median line in the posterior portion of the region, and (3) a row directly upon the median line with one or more rows on each side of the line. This region ends at or near the base of the uropygial gland. The lateral-pelvic region consists of a diagonal row or rows, lateral to the pelvic region, that originate in the dorsal region or anterior portion of the pelvic region and extend outward toward the femur.

For the few rows of small feathers that arise near the posterior margin of the scapula and extend posteriorly and laterally into the armpit, I propose the name lateral-scapular region.

### ACCIPITRIDAE

*Buteoninae. Buteo jamaicensis borealis* (fig. 2).—The lateral-cervical apteria are wide and definitely separate the two cervical regions. At their anterior margins these apteria curve ventrally and constrict the ventral-cervical region. The dorsal-cervical region is a continuation of the occipital and postauricular regions. In its anterior part it is as wide as the head, but it diminishes abruptly to about half this width and continues so to the trunk. At the base of the head the feathers are small and like those of the occipital region, but posteriorly they increase in size of shaft and reach their maximum development in the interscapular region.

Slightly past the base of the neck the cervical region divides to form the two branches of the interscapular region. These branches lie on each side of the median line and consist of three or four rows of stout feathers; they extend to a point slightly anterior to the origin of the posterior humeral patagium.

The dorsal region consists of a row of three or four feathers on each side of the median line. These feathers have much lighter shafts than those of the interscapular region.

The pelvic region is a continuation of the two rows of the dorsal region with the addition of one or two rows on each side and a row directly upon the median line. With the appearance of the median row the feathers become increasingly stout as the region extends posteriorly. They reach their greatest development just anterior to the uropygium, where the region is slightly wider than elsewhere. The last feather of the spinal tract is inserted at the base of the uropygial gland but not upon the body of the gland.

The lateral scapular region consists of two or three rows of small feathers originating at the posterior margin of the scapula and curving down into the armpit.

The lateral pelvic region consists of three rows which spring from the dorsal region and extend diagonally out on the sides to merge with the femoral tract near the head of the femur. The feathers of this region are similar in size to those of the dorsal region but much smaller than those of the pelvic region.

*Haliaeetus vocifer*.—In the pelvic region there is a single row of feathers upon the median line, with, as near as I could determine, two or three rows on each side of the median one.

*Haliaeetus leucocephalus washingtonensis*.—The dorsal region is like that of *Buteo*. The pelvic region consists of a row of feathers on the median line and three rows on each side of this median one.



Fig. 3. Dorsal surface of *Elanus leucurus majusculus*.



Fig. 4. Dorsal surface of *Ictinia mississippiensis*.

Elaninae. *Elanus leucurus majusculus* (fig. 3).—The dorsal-cervical and interscapular regions are, except for minor details, similar to those of *Buteo*. The dorsal-cervical region is supported by a more definite patagium, and the two branches of the interscapular region are farther apart.

The posterior half of the tract differs somewhat from that of *Buteo* but presents the same basic plan. There is a gap between the interscapular and dorsal regions, and the feathers of the latter are exceptionally small. The pelvic region is proportionately much wider than it is in *Buteo* and is almost uniform in width throughout its length. There are two or three rows of feathers on each side of the median row.

The lateral-pelvic region consists of a row on each side of the body. These originate near the dorsal region, extend about half the length of the pelvic region, and are parallel to the outer margin of the latter.

Perninae. *Elanoides forficatus forficatus*.—In the pelvic region there is a row of feathers on the median line and a single row on each side of this median one. There is no median row in the dorsal region.

Milvinae. *Ictinia mississippiensis* (fig. 4).—The dorsal-cervical, interscapular, and lateral-scapular regions are like those in *Buteo*.

The dorsal region consists of a single row on each side of the median line. Each row contains three small feathers spaced far apart. In the pelvic region these two rows continue, with the addition of a row on the median line, to the base of the uropygial gland. Near the uropygium an additional row is added on each side, but these soon disappear as the region tapers toward the uropygial gland. In the dorsal and pelvic regions the feathers gradually increase in size posteriorly.

The lateral-pelvic region originates lateral to the anterior margin of the pelvic region and consists of two parallel rows on each side of the body. The most anterior row is short and includes but two feathers. The second row is about 5 mm. posterior to the first and extends diagonally over the body to unite with the femoral tract at the latter's posterior margin at the base of the leg.

*Rostrhanus sociabilis plumbeus*.—The pelvic region is similar to that of *Ictinia*.

*Haliaeetus intermedius*.—In the pelvic region there is a row on the median line and, so far as I could determine, two rows of feathers on each side of the median one.

Accipitrinae. *Accipiter cooperii*.—The entire spinal tract is similar to that of *Buteo*. The diagonal rows of the lateral-pelvic region are more clearly defined.

*Meleagris metabates*.—In the pelvic region there is a single row on the median line, with one or possibly two rows on each side of it.

Aegyptiinae.—Nitzsch (1867, pl. II, fig. 2) figures the dorsal surface of *Gypaetus barbatus* and describes (*op. cit.*, p. 44) this tract in his text. He remarks: "The lower portion of the spinal tract is united to the above mentioned fork between the shoulders [interscapular region] by two converging rows of single feathers, and is then continued uninterruptedly as a narrow band along the dorsal vertebrae, to terminate at the oil-gland." He also describes *Sarcogyps calvus*, *Neophron percnopterus*, and *Aegyptus monachus* as having a spinal tract similar to the one in *Gypaetus barbatus*. It is apparent from his description that the spinal tract of the Aegyptiinae resembles that of the Buteoninae.

Circinae. *Circus cyaneus hudsonius*.—The dorsal-cervical region is similar to that in *Buteo* but is supported by a well-developed patagium. About halfway down the neck the ventral-cervical patagium unites with the dorsal-cervical patagium. The lateral margins of the interscapular region are curved and give this region a more nearly ovoid shape.

The posterior half of the spinal tract is similar to that found in *Ictinia*. The dorsal region is a row of three feathers on each side of the median line. These two rows, with an additional one on the median line, extend through the pelvic region. In the anterior portion of the pelvic region these rows lie close to the median one, but in the posterior portion they are slightly more lateral and give the region a wider appearance. At one point anterior to the uropygium there is an additional feather on each side; posterior to this the region tapers abruptly to the base of the uropygial gland.

The lateral-scapular region is not present. The lateral-pelvic region consists of a single row on each side of the body, originating slightly lateral to and at a point opposite the middle of the dorsal region and extending diagonally out. These rows do not reach the femoral tract but end anterior to it.

*Gymnogyps typicus* subsp. ?—In the pelvic region there is a row on the median line and one row on each side of it.

Circætinæ. *Terathopus ecaudatus*.—In the pelvic region there is a row of feathers on the median line and three or four rows on each side of this row.

*Spilornis cheela ricketti*.—In the pelvic region there is a row on the median line and three rows on each side of this central one.

#### FALCONIDAE

Falconinae. *Falco mexicanus* (fig. 5).—The dorsal-cervical region is similar to that of *Buteo*, but the cervical patagium is less apparent. The interscapular region extends the same distance as in *Buteo* and contains about the same number of rows, but the feathers are closer together and the branches narrower.

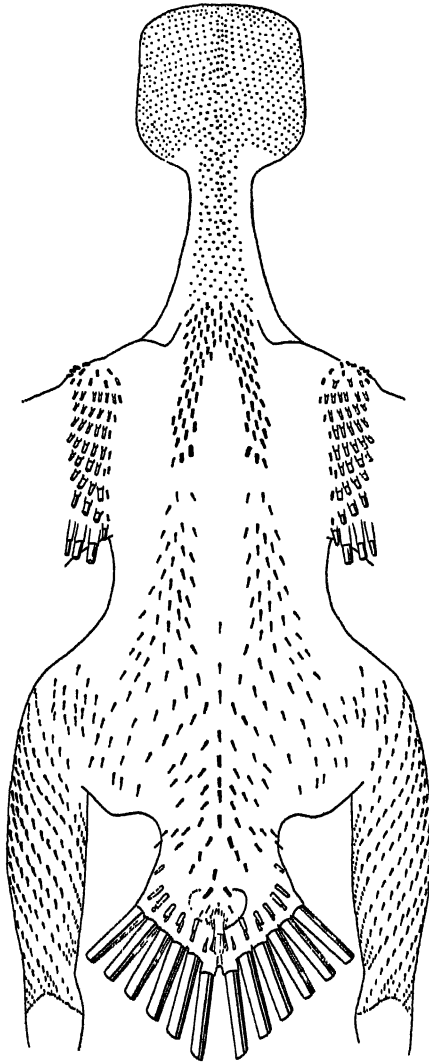


Fig. 5. Dorsal surface of *Falco mexicanus*.

The dorsal region consists of two or three rows of scattered feathers on each side of the median line. These areas continue in the pelvic region, and the feathers, besides being in longitudinal rows, are arranged in diagonal rows directed toward the legs. In the dorsal and pelvic regions the first row lateral to the median line is much farther from this line in *Falco* than is the corresponding row in any of the *Accipitridae* examined. This fact together with the lateral extension of the areas makes it impractical to distinguish a lateral-pelvic region in the *Falconidae*. At the anterior margin of the synsacrum a row of feathers appears on the median line and continues posteriorly through the pelvic region. A short distance anterior to the uropygium the pelvic region begins to narrow, and then it gradually tapers toward the uropygial gland. The last feather of the spinal tract is inserted on the body of this gland. In the middle portion of the pelvic region the diagonal rows extend to the femoral tract and blend with it.

The lateral-scapular region is not well marked and its feathers are downlike.

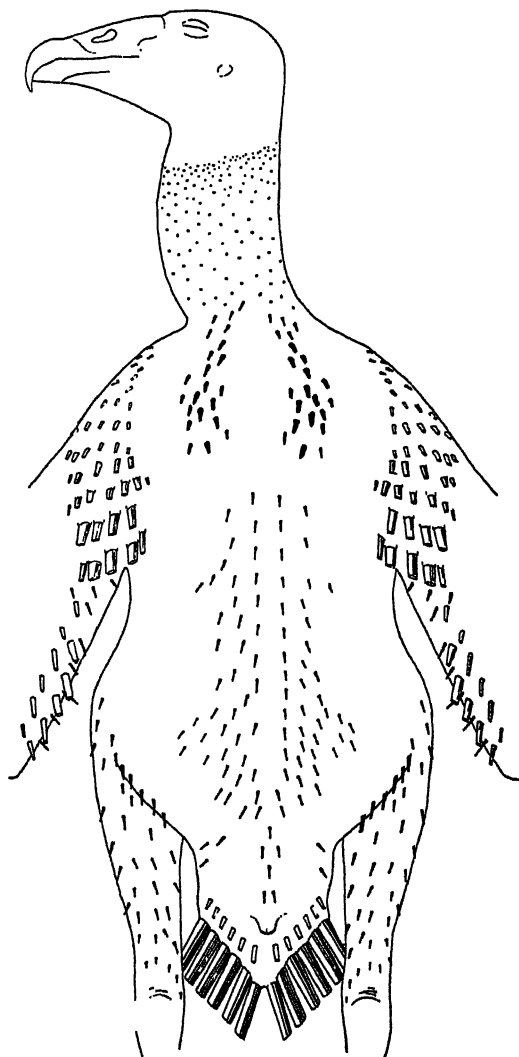


Fig. 6. Dorsal surface of *Cathartes aura teter*.

*Falco rusticolus candicans* and *Falco peregrinus anatum*.—The pelvic region in these two forms is the same as that in *Falco mexicanus*.

*Falco sparverius sparverius*.—The whole spinal tract is a miniature of *F. mexicanus*.

Herpetotherinae. *Microstus semitorquatus naso*.—The dorsal and pelvic regions are similar to those in *F. mexicanus*.

Polyborinae. *Phalcoboenus albogularis*.—The dorsal and pelvic regions are similar to those in *F. mexicanus* except that each lateral branch apparently consists of only two rows of feathers.

*Polyborus plancus plancus*.—The dorsal and pelvic regions appear to be the same as those in *F. mexicanus*.

#### SAGITTARIDAE

*Sagittarius serpentarius*.—In the pelvic region there is a row of small feathers on the median line and two rows on each side of this central one. In the posterior part of this



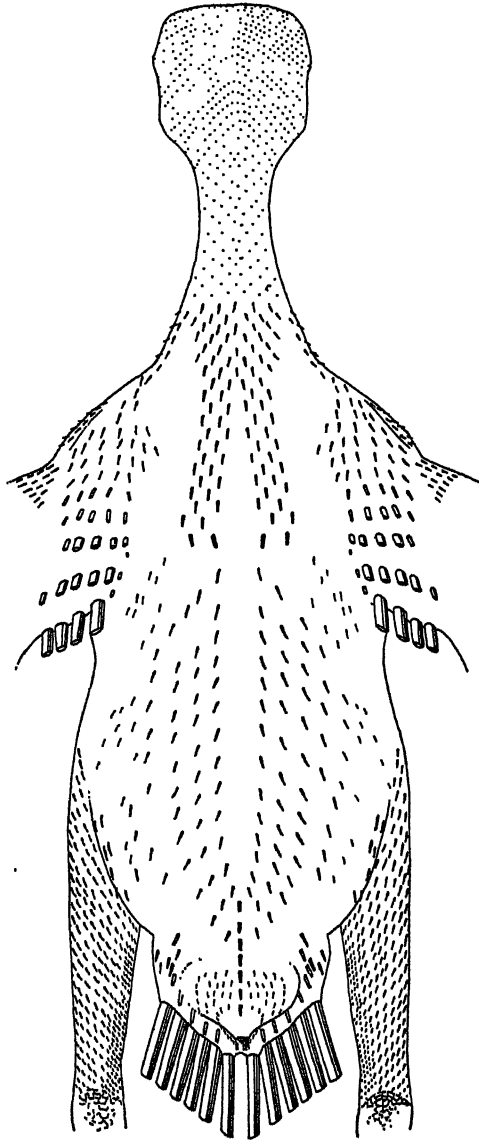


Fig. 7.—Dorsal surface of *Pandion haliaetus carolinensis*.

region a third row is added to each side. The median and lateral rows originate simultaneously, and probably their anterior part represents the dorsal region. Nitzsch (1867, p. 63) describes the pelvic region as two parallel rows. Apparently he overlooked the row of small feathers on the median line.

#### CATHARTIDAE

*Cathartes aura teter* (fig. 6).—The hairlike feathers of the head are continued down the neck for approximately one-fourth its length and are then replaced by plumaceous feathers. For an additional one-fourth of the neck the dorsal- and ventral-cervical regions are united, but the narrow lateral apteria appear at this point and separate the two regions along the

rest of the neck. The dorsal-cervical region covers all the dorsal surface of the neck and in this respect differs distinctly from the condition in the same region in *Buteo* and *Falco*. It is closely set with small feathers in its anterior portion, but posteriorly these become larger and farther apart.

At the point where the neck inserts in the trunk the cervical region divides to form the two branches of the interscapular region. These branches are similar to those of the Falconidae and Accipitridae but do not extend so far posteriorly. They consist of four or five rows of stout feathers. I find no lateral-scapular region.

The dorsal region consists, anteriorly, of one row on each side of the median line. It then increases to two rows on each side. These rows are a direct continuation of the interscapular region, but their feathers are only one-fourth the size of those of the latter region. The dorsal and pelvic regions fuse and continue toward the tail; a narrow apterium extends down the median line and divides the right and left portions of these two regions.

The pelvic region consists of a wide area of three to four vertical rows on each side of the median line. Near the uropygium these two branches curve inward and unite. They then continue as three rows. The region ends slightly anterior to the uropygial gland.

The entire spinal tract, after the beginning of the plumaceous feathers, shows a definite likeness to that of *Pandion*.

#### PANDIONIDAE

*Pandion haliaetus carolinensis* (fig. 7).—The lateral-cervical apteria are very narrow, about five millimeters or less in width throughout most of their length. Although the dorsal and ventral-cervical regions do not meet, they sometimes appear to do so because of the extreme narrowness of the apteria.

The dorsal-cervical region is a continuation of the occipital and postauricular regions at the base of the head. The anterior half of this region is wide and covers the dorsal and lateral surfaces of the neck; it consists of small feathers similar to those that are found in the occipital region. In its posterior half this region narrows slightly and the feathers increase in size as the region approaches the base of the neck. At this point the tract divides and forms the two branches of the interscapular region.

The branches of the interscapular region lie close to, and on each side of, the median line. Each branch consists of three or four rows of stout feathers and ends anterior to the proximal origin of the posterior-humeral patagium.

The dorsal region is a continuation of the spinal tract, but the feathers are much reduced in size in comparison to those of the interscapular region. It is short and so blends with the pelvic region that it is not practical to distinguish the two.

The pelvic region consists of two wide areas, one on each side of the body; these taper inward on their outer margins until they come together a short distance anterior to the uropygium. The last feather of the tract inserts in the body of the uropygial gland. Each of these branches consists of four to five vertical rows; the feathers of each row are inserted slightly posterior to those which are medial to them, so that the whole area presents diagonal as well as vertical rows. The feathers increase in size as the region progresses posteriorly.

The lateral-scapular region consists of three or four rows of small feathers, arising near the posterior margin of the scapula and extending posteriorly and downward into the armpit.

In the anterior portion of the pelvic region two of the diagonal rows continue onto the lateral surface and unite with the femoral tract at its dorsoposterior margin. These rows constitute the lateral-pelvic region.

#### THE VENTRAL TRACT

##### DEFINITIONS

The ventral tract extends from the submalar region posteriorly over the neck, breast, and abdomen, and ends at or slightly anterior to the anus. It consists of five areas, the ventral-cervical, sternal, axillar, subaxillar, and abdominal

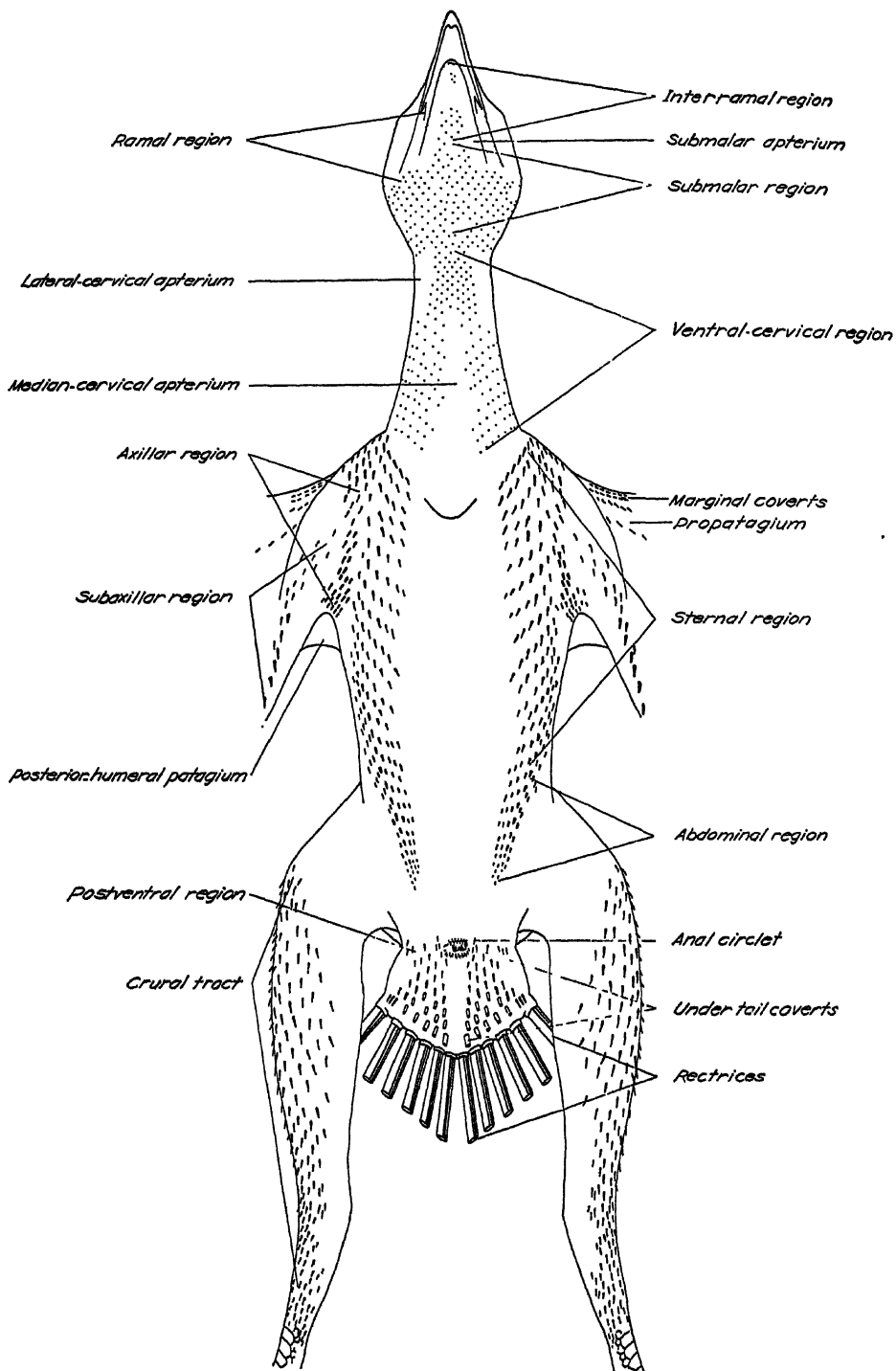


Fig. 8. Tracts and regions of ventral surface of *Buteo jamaicensis borealis*.

regions, which, with the exception of the anterior portion of the cervical region, are divided into right and left branches.

The ventral-cervical region extends along the lower surface of the neck from the submalar region to the interfurcular space. It usually occurs as a single tract in its anterior portion and as a right and left branch in its posterior portion. At each shoulder a narrow continuation from the ventral-cervical region passes onto the trunk and sends branches to the humeral tract, to the marginal coverts of the alar tract, and to the sternal and axillar regions of the ventral tract.

The sternal region extends down each side of the breast and ends at the posterior margin of the sternum. The abdominal region is a continuation of the sternal region and proceeds posteriorly over the abdominal surface to end at or near the anus. The axillar region branches from the anterior portion of the sternal region and extends laterally to the armpit.

The region that originates on the anterolateral surface of the breast and extends along the lower surface of the humerus, I call the subaxillar region. The feathers which are ordinarily referred to as "axillars" rise from both the axillar and the subaxillar region, but in most hawks there is a definite break between these two regions, and, for simplification of discussion, it appears best to use two names in referring to them.

#### ACCIPITRIDAE

*Buteoninae. Buteo jamaicensis borealis* (fig. 8).—The lateral-cervical apteria curve inward at the throat and restrict the anterior portion of the ventral-cervical region to a narrow area that extends about a quarter of the distance down the neck. At this point the region divides and continues to the interfurcular space as two branches with a wide median cervical apterium between them. Each branch is wide, and in its posterior half the feathers are inserted in the lateral-cervical patagium. Near the base of the neck a short ridge from this patagium extends diagonally into the interfurcular space, and the cervical region terminates upon this ridge. In the anterior unbranched portion of the cervical region the feathers are small shafted and similar to those of the adjoining submalar region; after the region branches, the feathers increase in size and remain large throughout the rest of the region.

A narrow continuation of the cervical region extends from the lateral margin of each branch along the edge of the parapatagium to the shoulder, where it divides and sends branches to the dorsal and ventral surfaces of the trunk.

The sternal region consists of a wide band on each half of the breast but at some distance from the median line. Each branch starts at the shoulder as a narrow tract. This gradually widens as it extends half the length of the furcula and then continues posteriorly over the breast. The width of the tract varies from five to seven rows of feathers.

At a point nearly opposite the anterior end of the keel the axillar region branches slowly from the sternal region and curves laterally into the armpit. It consists of four to five rows of feathers slightly heavier than those of the sternal region. The axillar region ends at the armpit and does not extend onto the humerus as it does in *Pandion*. The feathers of the subaxillar region start as three rows on the lateral surface of the breast, anterior to the axillar region, and extend onto the lower surface of the humerus. The number of rows diminishes until there is but one left, the three central feathers of which have enlarged shafts.

The branches of the sternal region narrow gradually as they extend posteriorly over the pectoral muscles and continue to do so through the uninterrupted continuation of the tract in the abdominal region. The abdominal region extends from the posterior margin of the

sternum to a point about three fourths the distance over the abdomen, where it terminates as a narrow pointed area. Throughout the sternal and abdominal regions the feathers are more heavily shafted in the ventral part than on the lateral margins of the regions.

Elaninae. *Elanus leucurus majusculus* (fig. 9).—The ventral cervical region is like that of *Buteo*, as is also the general appearance of the sternal and axillar regions. The latter two regions differ from *Buteo* in two respects: there is a greater difference between the types of feathers in them, and the axillar region does not extend to the armpit. The feathers of the axillar region have shafts about twice the size of those in the sternal region. The axillar region ends medial to the armpit, and a single row of feathers extends from it along the



Fig. 9. Ventral surface of *Elanus leucurus majusculus*.



Fig. 10. Ventral surface of *Ictinia mississippiensis*.

posterior margin of the breast to the humerus. The abdominal and the subaxillar regions are the same as in *Buteo*.

Milvinae. *Ictinia mississippiensis* (fig. 10).—The general outlines of the regions of the ventral tract are similar to those in *Buteo*. The division of the axillar and sternal regions occurs more posteriorly, and the axillar region does not reach the armpit.

Accipitrinae. *Accipiter cooperii*.—The ventral-cervical region is like that of *Buteo*, but the sternal and axillar regions differ from those of the latter species. The division of these two regions occurs anterior to the keel, and the axillar region turns laterally more acutely, with the result that these regions are more widely separated than in *Buteo*. The axillar, sternal, and abdominal regions are all narrower and contain fewer rows of feathers. The axillar region ends at about the same point in the armpit as it does in *Buteo*.

Circinae. *Circus cyaneus hudsonius*.—The ventral-cervical and subaxillar regions are like those in *Buteo*. All the regions of the ventral tract on the trunk are narrower and contain fewer rows of feathers. The axillar springs from the sternal region at about the same point as it does in *Buteo* but curves away more abruptly, leaving a wider apertium between it and the sternal region. It ends in a similar position in the armpit. The abdominal region contains only three rows at its widest part and narrows to a single row.

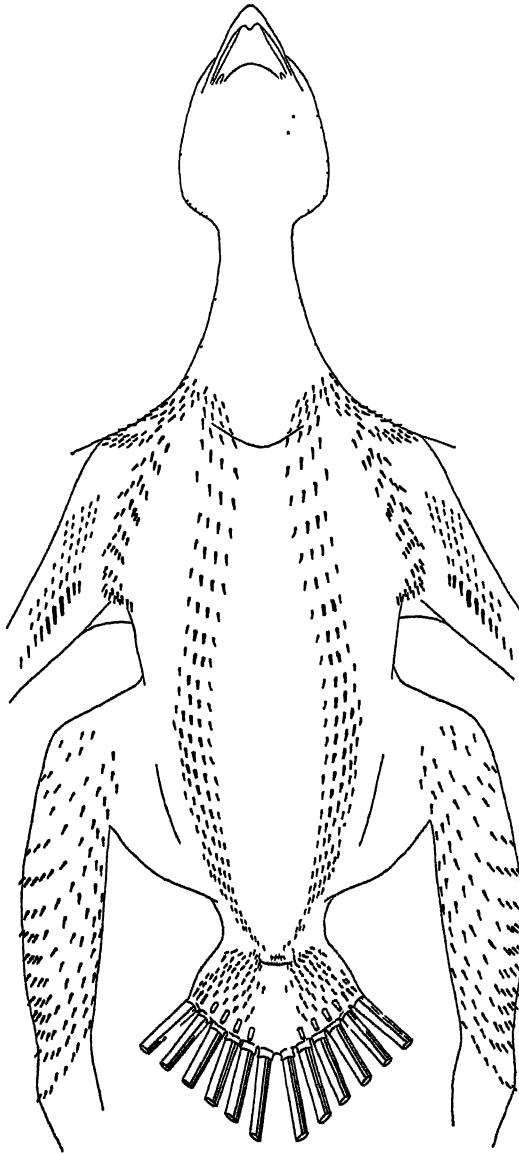


Fig. 11. Ventral surface of *Falco mexicanus*.

#### FALCONIDAE

*Falco mexicanus* (fig. 11).—The ventral-cervical region is similar to that of *Buteo* except that it continues onto the trunk without narrowing, and that there is no extension into the interfurcular space. At the shoulder the sternal and axillar regions spring independently from the cervical region, and they are not united at any point thereafter. In this respect especially the ventral tract differs greatly from that found in the family Accipitridae.

The sternal region progresses down the furcula almost to the median line and then extends posteriorly and swings gradually outward over the breast. This region ends at the posterior margin of the sternum; the ventral tract is continued by the abdominal region. The right

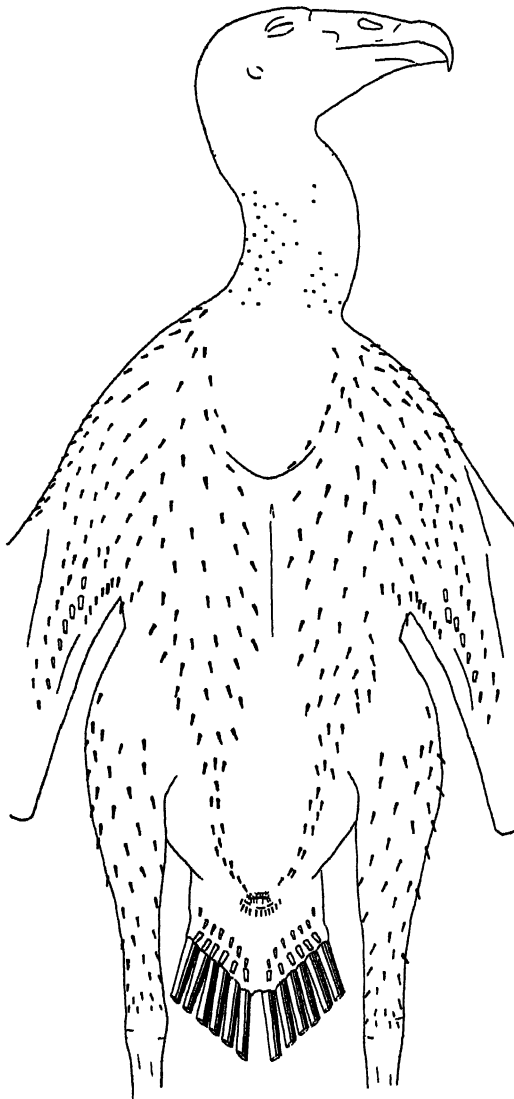


Fig. 12. Ventral surface of *Cathartes aura teter*.

and left halves of the latter region extend down each side of the abdomen and, in their posterior part, curve inward and almost unite anterior to the anus. Throughout their entire length the sternal and abdominal regions form a narrow band which usually does not contain more than five rows.

The axillar region is a narrow band of about six rows extending posteriorly and slightly diagonally from the shoulder to the armpit. Its feathers are larger in the median rows than in the lateral rows. The anterior part of the subaxillar region consists of five or six rows of small feathers on the lateral surface of the breast. These rows decrease in number, as the region continues down the humerus, until there remains but a single row. The subaxillar region is more highly developed than it is in any of the Accipitridae.

*Falco sparverius sparverius*.—The ventral tract is like that of *F. mexicanus*.

## SAGITTARIIDAE

*Sagittarius serpentarius*.—Because of the "make" of the skin I was unable to determine the character of the ventral tract in this species. Neither am I able to make anything out of Nitzsch's description of this tract (1867, p. 63). Apparently it resembles the one found in the family Accipitridae, but it may present differences.

## CATHARTIDAE

*Cathartes aura teter* (fig. 12).—The anterior portions of the dorsal- and ventral-cervical regions consist of fine hairlike feathers like those covering the head; the plumaceous feathers begin at a point one-fourth the distance down the neck. The dorsal and ventral regions are connected for about one-half the length of the neck. Posteriorly from this point a narrow lateral-cervical apterium separates the two regions.

The plumaceous portion of the ventral-cervical region consists of two halves which are completely separated by a wide ventral-cervical apterium. Each branch is closely set with small feathers in its anterior portion, but posteriorly the feathers become larger and more scattered. The cervical branches narrow as they reach the interfurcular space and a narrow band continues on each side to the shoulder, where each sends branches to the dorsal and ventral surfaces.

The ventral branch spreads immediately over the entire surface of the pectoral muscles, leaving only a narrow apterium along the median line. The feathers of this pectoral area are set at wide intervals and arranged in vertical and diagonal rows. They are largest through the middle portion of each side and become smaller on the lateral surfaces. There is no differentiation between the axillar and sternal regions, or between the axillar and subaxillar regions.

There is no apterium in the body of each branch of the sternal region as was stated by Nitzsch (1867, p. 51).

The subaxillar region extends the length of the humerus and onto the anterior surface of the breast. Its posterior row of heavy feathers extends along the humerus and curves into the axillar region. The axillar region sends a single row through the armpit to extend a short distance on the internal surface of the humerus beneath the subaxillar region. This condition is similar to that found in *Pandion* but does not occur in any of the Accipitridae or Falconidae.

The thigh, throughout its length, is attached to the trunk. The lateral margin of the sternal region curves inward from the armpit, and the region continues to the posterior margin of the sternum. In the abdominal region the tract narrows rapidly, and it swings slightly toward the median line before ending just anterior to the anus.

## PANDIONIDAE

*Pandion haliaetus carolinensis* (fig. 13).—The ventral-cervical region extends solidly over the ventral surface of the neck from the submalar region to the interfurcular space. The median-cervical apterium, which in most falconiforms extends at least half the length of the neck, is represented in *Pandion* by a small notch in the middle of the posterior margin of the cervical region. At its anterior margin this region fuses with the postauricular and submalar regions, but it is separated throughout its entire length from the dorsal-cervical region by the narrow lateral-cervical apteria. The feathers of its anterior portion are small, similar to those of the submalar and postauricular regions, whereas those of the posterior half have large, stiff shafts.

At the interfurcular space a narrow branch continues, on the lateral-cervical patagium, from the lateral margins of the cervical region to the shoulder. At this point it divides and sends one branch to the dorsal and one to the ventral surface.

The sternal and axillar regions spread over the entire ventral and lateral surfaces of the breast and leave only a narrow apterium along the median line. These two regions are completely fused and there is no differentiation between the two in any respect. The only



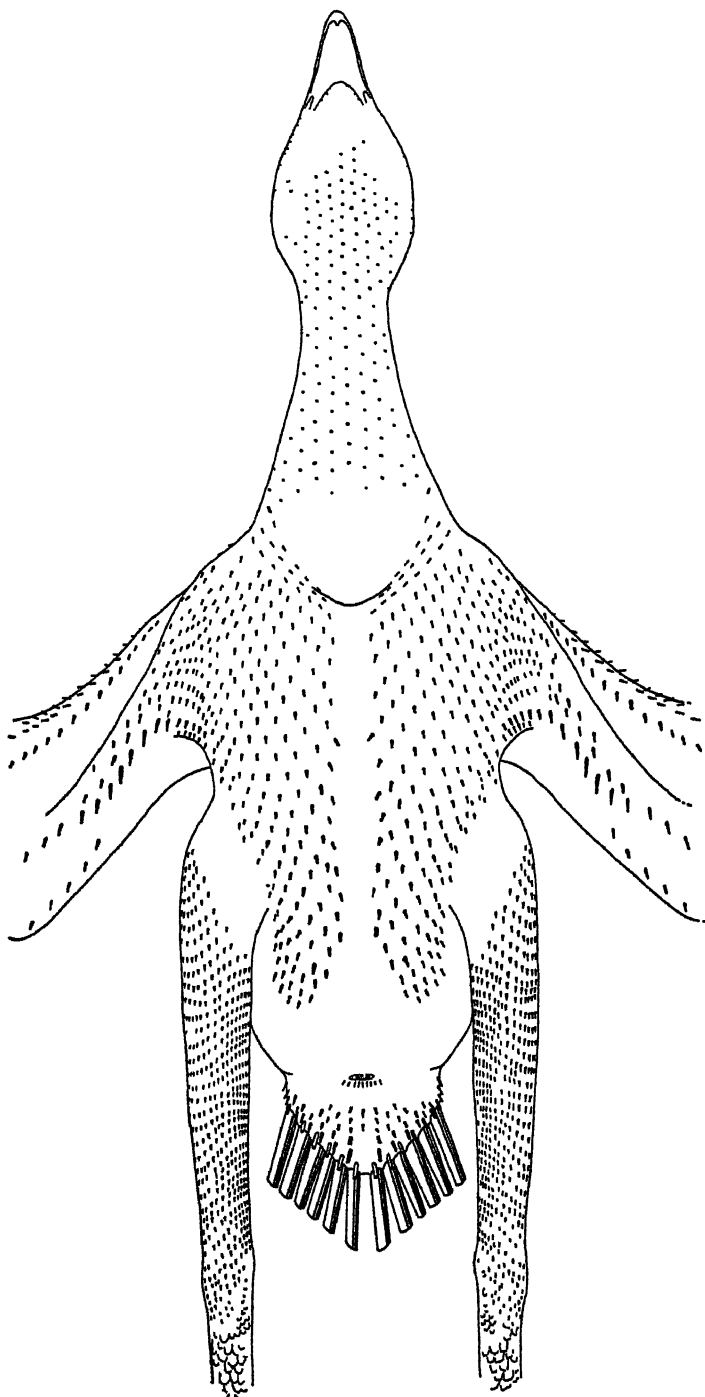


Fig. 13. Ventral surface of *Pandion haliaetus carolinensis*.

feathers that differ greatly from the rest of the area are the axillars, which are two rows of large-shafted feathers extending from the armpit down the ventral surface of the humerus. The feathers on the anterolateral surface, where the axillar and subaxillar regions fuse, are more numerous and smaller than those nearer the median line. The feathers of the area as a whole tend to increase in size as the tract progresses posteriorly. The rows of feathers constituting the axillars curve smoothly out in unbroken sequence from the axillar region into the subaxillar region, and extend about three-fourths the length of the humerus.

The thigh is attached throughout its length to the trunk, and the knee lies nearly flush with the breast. The lateroposterior margin of the sternal region curves round the knee and the tract then extends posteriorly as the abdominal region. The abdominal region is a narrowed continuation of the ventral tract, and gradually terminates in a point about three-fourths the distance down the abdomen.

## THE CAUDAL TRACT

### DEFINITIONS

The caudal tract consists of the rectrices, upper tail coverts, lower tail coverts, postpelvic region, tuft and covering of the uropygial gland, postventral region, and anal circlet. The rectrices are the principal tail feathers and are twelve in number in all the species examined. The outer five pairs are inserted in a diagonal row along the posterior margin of the uropygium, and the middle pair is above this row and slightly overlaps the second pair. The single row of upper tail coverts is inserted on a line parallel with that of the rectrices. The postpelvic region is a small group of feathers on each side of the uropygium at its dorsolateral margin and near its base. The tuft of the uropygial gland encircles the tip of the papilla of this gland. The body of the gland may or may not have a scattering of downlike feathers.

In most of the hawks there are numerous rows of lower tail coverts. The row nearest the rectrices I consider as the major under tail coverts and the remaining rows as the minor under tail coverts. The anal circlet consists of small feathers surrounding or partly surrounding the anus. A narrow apterium usually extends from the anal circlet to the middle pair of rectrices and separates the right and left lower tail coverts. This may be known as the midcaudal apterium. The postventral region is a small area on either side of the anus.

### ACCIPITRIDÆ

*Buteoninae. Buteo jamaicensis borealis* (figs. 2, 8).—The basal parts of the calami of the rectrices are enclosed in a patagium. There are six pairs of upper tail coverts. The postpelvic region consists of a group of three feathers.

The tip of the papilla of the uropygial gland is encircled with modified down feathers and the body of the gland is covered with down feathers that are less modified than those of the tuft and much more downlike than those covering the gland in *Pandion*.

There are 7 or 8 major lower tail coverts inserted in a row which is parallel to and does not extend beyond the row of rectrices. The minor lower tail coverts consist of six diagonal rows. The first row has 6 or 7, the second 5, the third 4 or 5, the fourth 4 or 5, the fifth 4, and the sixth 3 feathers.

The anus is not encircled with feathers, but there are one or two rows along its lateral margins. The postventral region consists of a few scattered contour feathers.

*Elaninae. Elanus leucurus majusculus* (figs. 3, 9).—There are six upper tail coverts. With

the single exception of *Pandion*, the uropygial gland in this species is proportionately much larger than in any other falconiform examined. It is 13.8 mm. wide at its base and 14.4 mm. long. The gland tapers posteriorly and has the shape of a truncated cone. The papilla is so small that it can hardly be detected; the papilla tuft consists of ten feathers 2.5 mm. long. The body of the gland is devoid of down feathers except for a few along its basal and lateral margins. The postpelvic region consists of two feathers, the one anterior to the other.

The six major lower tail coverts are inserted as in *Buteo*. The minor lower coverts consist of six or seven diagonal rows placed as in *Buteo*, but each row usually has fewer feathers. The anal circlet occurs only on the anterior and lateral margins of the anus. The postventral region consists of a few feathers lateral to the anal circlet.

Milvinae. *Ichthyophaga mitsis* (figs. 4, 10).—There are six upper tail coverts. The postpelvic region is like that of *Elanus*. The uropygial gland is 9.7 mm. wide and 8.0 mm. long. Its tip is encircled with modified down feathers and there is a scattering of down over the body of the gland, but there is less of it than in *Buteo*.

The ventral-caudal tract is like that of *Buteo* in its general features. There are seven major lower tail coverts and six to seven rows of minor coverts. The number of feathers in the rows of minor coverts is similar to that of *Buteo*. The anal circlet completely surrounds the anus. The postventral region is absent.

Accipitrinae. *Accipiter cooperii*.—In the general features of the tract this species is similar to *Buteo*. There are six upper tail coverts. The uropygial gland is comparatively small, 10.8 mm. wide and 7.8 mm. long; its tuft and covering of down is similar to that of *Buteo*. The postpelvic region consists of five feathers.

There are six major under tail coverts and six or seven rows of minor coverts. The anal circlet extends along the lateral and posterior margins of the anus but not along the anterior margin. The postventral region consists of a few scattered small feathers.

Circinae. *Circus cyaneus hudsonius*.—The general aspects of both surfaces of the caudal tract are like those of *Buteo*. The postpelvic region consists of two feathers. The uropygial gland is 8.6 mm. wide and 7.4 mm. long. The papilla is tufted and a few down feathers are scattered over the body of the gland.

There are six major under tail coverts and six or seven rows of minor coverts. The anal circlet does not surround the anus but occurs only along its lateral margins. There is a scattering of feathers on either side of the anus, which constitutes the postventral region.

#### FALCONIDAE

*Falco mexicanus* (figs. 5, 11).—As in the hawks of the family Accipitridae, the bases of the rectrices are enclosed in a patagium. There are five upper tail coverts. The postpelvic region consists of four or five scattered feathers.

The uropygial gland is proportionately somewhat larger than in most of the Accipitridae; it is 15.7 mm. wide and 11.4 mm. long. The papilla is long and the tip is not only encircled with feathers but is entirely covered with them. The papilla itself is 5 mm. long, and the tuft feathers 11.8 mm. long. The body of the gland is covered with down feathers with highly modified stiff shafts.

There are seven major under tail coverts. The anal circlet, postventral region, and minor under coverts blend with one another along the ventral surface of the uropygium. The anal circlet occurs only along the lateral margins of the anus. The postventral region extends a short distance laterally from the anus. There are five or six diagonal rows of minor lower tail coverts.

#### CATHARTIDAE

*Cathartes aura* (figs. 6, 12).—The rectrices are inserted directly into the body of the uropygium; their basal portions are not enclosed in a patagium. There are six upper tail coverts. The postpelvic region consists of two feathers. The measurements of the gland cannot be taken in the specimen at hand. There is no tuft on the papilla and no down feathers on the body of the gland.

There are six major under tail coverts. The minor coverts consist of a single row of six

feathers parallel with the row of major coverts. There is an occasional feather or two in the area anterior to the minor coverts. The anal circle extends only along the lateral and posterior margins of the anus.

#### PANDIONIDAE

*Pandion haliaetus carolinensis* (figs. 7, 13).—The rectrices insert directly into the body of the uropygium; the basal portions of their calami are not enclosed in a patagium. There are six feathers which may be definitely considered upper tail coverts; these are inserted in a row which is approximately parallel to that of the rectrices. At the anterior end of the row of upper coverts are two or three feathers that are usually in the same plane as the coverts, although sometimes offset slightly above or below this plane. These feathers are similar to the upper coverts and it is reasonable to consider them as belonging to the same series, in which case the number of coverts can be considered to be eight or nine. Clark (1918, p. 121) found them to be seven or eight. Dorsal to these outer coverts are two feathers that are similar in nature and function to the coverts. These may represent the remains of a second row of upper tail coverts, but it is probably best to consider them as homologous with the post-pelvic region of other hawks.

The most posterior feather of the spinal tract inserts either on the body of the uropygial gland or just at its base. The tuft of the uropygial gland consists of a single row of modified down feathers encircling the tip of the papilla. In one specimen there were 11 of these feathers; in another, 14. The body of the gland has a scattered covering of modified down feathers similar to those of the tuft.

There are eight or nine major lower tail coverts. While this row of coverts is beneath the rectrices it runs parallel with them, but after passing beyond the insertion of the most lateral rectrix it curves dorsally.

Anterior to the major lower coverts are five rows of minor lower coverts parallel to the row of major under coverts. The first row of minor coverts consists of 7 or 8, the second of 7 or 8, the third of 5 or 6, the fourth of 3, the fifth of 1 or 2 feathers. The midcaudal apterium is narrower than in either *Buteo* or *Falco* and only extends anteriorly as far as the third row of the minor coverts.

The anal circle consists of a row of small contour feathers along the posterior margin of the anus. There is no postventral region.

### THE HUMERAL TRACT

#### DEFINITIONS

The humeral tract arises at the base of the neck from the ventral-cervical region. This tract progresses but a short distance over the shoulder before a narrow branch springs from it and becomes the marginal coverts. The humeral tract extends about one-half the length of the dorsal surface of the humerus and ends on the posterior margin of the posterior-humeral patagium. Its feathers increase in size as the tract extends posteriorly and are arranged in four to six longitudinal rows and a variable number of transverse rows. The humeral tract varies but little and presents a similar appearance in most of the falconiforms. The tertiaries arise along the posterior margin of the humerus and are the remiges of the upper arm. They thus belong to the alar tract and are not to be confused with the humeral tract.

#### ACCIPITRIDAE

*Buteo jamaicensis borealis* (fig. 2).—The humeral tract extends one-half the length of the humerus and ends upon the posterior margin of a well-developed posterior-humeral patagium. It is a narrow tract with its feathers spaced close together. There is a wide apterium between this tract and the lesser coverts of the alar tract. The transverse rows are

approximately at right angles with the long axis of the tract. The most posterior of these rows has five feathers, the outer four of which are large.

The characters of this tract remain unchanged throughout the other forms examined in this family (figs. 3, 4).

#### FALCONIDAE

*Falco mexicanus* (fig. 5).—This tract extends one-half the length of the humerus and ends upon the posterior margin of a well-developed posterior-humeral patagium. Its anterior origin on the trunk is more lateral than in *Buteo*, and its feathers are more closely set than in the latter species. The transverse rows, instead of being at right angles with the long axis of the tract as they are in *Buteo*, extend diagonally lateroanteriorly. There are four feathers in the most posterior row, the inner feather a small one and the outer three large.

The dorsal branch of the marginal coverts springs from the humeral tract at a point posterior to that from which it arises in *Buteo*, and the apterium between the dorsal and ventral branches of the marginal coverts is larger than it is in the latter species.

There is a wide apterium between the humeral tract and the lesser coverts of the alar tract.

#### CATHARTIDAE

*Cathartes aura teter* (fig. 6).—Since there is no posterior-humeral patagium in this species, the humeral tract ends upon the body of the upper arm. It is a wide tract of widely spaced feathers and extends about one-third the length of the humerus. The transverse rows are similar to those of *Pandion* since they extend diagonally lateroposteriorly. The last transverse row consists of six feathers, the outer two small and the inner four large. The apterium between the humeral tract and the lesser coverts is so narrow that it is hardly discernible.

#### PANDIONIDAE

*Pandion haliaetus carolinensis* (fig. 7).—The humeral tract extends one-third the length of the humerus. It is a wide area of almost uniform breadth, with its feathers spaced far apart. The lesser coverts on the alar patagium and the humerus are separated from the humeral tract by a narrower apterium than in either *Buteo* or *Falco*. The posterior-humeral patagium upon which this tract ends is less developed than it is in either the Accipitridae or the Falconidae. The transverse rows extend diagonally lateroposteriorly. The last transverse row consists of five feathers, the outer four of which are large.

### THE ALAR TRACT

#### DEFINITIONS

The alar tract includes all the feathers of the wing except those found in the humeral tract and the subaxillar region. The flight feathers or remiges consist of three series, the primaries, secondaries, and tertiaries.

All falconiforms have eleven primaries, the eleventh or most distal one vestigial. The first row of feathers above the primaries comprises the ten greater primary coverts, which lie between and distal to the primaries. Above these are the middle primary coverts, which vary in number and insert on the proximal side of the greater coverts. There is a variable number of rows of marginal coverts along the anterior edge of the manus. The first row beneath the primaries comprises the eleven greater under primary coverts, each of which lies proximal to its remex. Anterior to these coverts is the row of middle lower primary coverts. They vary in number and insert on the proximal sides of their remiges. The marginal coverts extend onto the ventral surface.

The number of secondaries varies from 15 to 20 in the species examined.

The wing is diastataxic throughout the Falconiformes. The number of remiges and coverts in each species is given in table 1.

The feathers of the first row above the secondaries are the greater upper secondary coverts. Except for a few at the proximal end of the series, each of these coverts inserts with its base proximal to its respective secondary and with its calamus extending diagonally to the distal side of the secondary. The middle upper secondary coverts lie anterior to and between the greater cov-

TABLE 1  
NUMBER OF REMIGES AND COVERTS IN EACH SPECIES

|                                       | Primaries | Greater upper primary coverts | Middle upper primary coverts | Greater under primary coverts | Secondaries | Greater upper secondary coverts | Greater under secondary coverts | Alula quills | Alula claw    | Carpal remex | Carpal coverts |
|---------------------------------------|-----------|-------------------------------|------------------------------|-------------------------------|-------------|---------------------------------|---------------------------------|--------------|---------------|--------------|----------------|
| <i>Buteo j. borealis</i> .....        | 11        | 10                            | 5                            | 11                            | 17          | 18                              | 17                              | 5            | —             | +            | +              |
| <i>Ictinia mississippiensis</i> ..... | 11        | 10                            | 7                            | 11                            | 16          | 17                              | 16                              | 4            | —             | +            | +              |
| <i>Accipiter cooperii</i> .....       | 11        | 10                            | 7                            | 11                            | 15          | 17                              | 15                              | 5            | —             | +            | +              |
| <i>Circus c. hudsonius</i> .....      | 11        | 10                            | 7                            | 11                            | 15          | 16                              | 16                              | 5            | —             | +            | +              |
| <i>Falco mexicanus</i> .....          | 11        | 10                            | 7                            | 11                            | 16          | 17                              | 15                              | 5            | +<br>Curved   | +            | +              |
| <i>Cathartes a. teter</i> .....       | 11        | 10                            | 8                            | 11                            | 18          | 19                              | 18                              | 4            | +<br>Straight | —            | +              |
| <i>Pandion h. carolinensis</i> .....  | 11        | 10                            | 8-9                          | 11                            | 20          | 20                              | 20                              | 4            | +<br>Straight | +            | +              |

Symbols: + indicates presence; — indicates absence.

erts. Each inserts on the distal side and at the tip of the calamus of its respective secondary. The lesser upper secondary coverts consist of a variable number of rows on the humeral patagium. The marginal coverts consist of numerous closely set rows along the anterior margin of the patagium. The greater under secondary coverts lie proximal to their secondaries and usually approximate the secondaries in number. There is a variable number of rows of middle and lesser under coverts, and the marginal coverts extend onto the ventral surface. In all species except *Cathartes a. teter* the calami of the secondaries are surrounded by a patagium and have elongate depressions between them. In *Cathartes* there are no depressions and the calami are enclosed within the solid structure of the forearm.

Between the series of primaries and secondaries there is usually a carpal remex with greater and middle upper coverts and a greater lower covert.

Along the posterior margin of the humerus is a row of tertiaries with two

rows of under coverts and one row of upper coverts. The tertiaries reach their greatest development in the middle of the series. The tertiaries are not a continuation of the secondaries but are homologous with the lesser upper secondary coverts. The row that is homologous to the secondaries is the second row of under tertial coverts (middle under tertial coverts).



Fig. 14. Full ventral surface of *Buteo jamaicensis borealis*.

The alula has four quills (alulas), with a tiny vestigial fifth or distal quill present in some forms. A variable number of greater upper alula coverts are inserted distal to their quills. There are two under coverts, the first inserted between the second and third quills and the second between the third and fourth quills. Marginal coverts extend over the dorsal and ventral margins. In certain forms a claw is present on the tip of the pollex.

#### ACCIPITRIDAE

*Buteo jamaicensis borealis* (fig. 14).—A wide propatagium extends from the shoulder to the distal end of the ulna; its entire surface is clothed with curved rows of lesser coverts.

The carpal remex is small, about one-third the size of the greater upper covert of the first secondary. The greater upper covert of the carpal remex is smaller than the adjoining covert of the first secondary but its middle upper covert is similar to that of the secondary. The greater under covert is proximal and between the greater and middle under coverts of the first primary.

The alula has a vestigial fifth quill; there is no claw on the pollex.

## FALCONIDAE

*Falco mexicanus*.—A wide propatagium, similar to the one in the Accipitridae, extends from the shoulder to the distal end of the ulna. Its entire surface is also clothed by definite rows of lesser coverts.

The carpal remex and its coverts are developed like those in *Buteo*. There is a vestigial fifth alula quill and the pollex bears a strongly curved claw 6.4 mm. in length.



Fig. 15. Full ventral surface of *Cathartes aura teter*.

## CATHARTIDAE

*Cathartes aura teter* (fig. 15).—The wing of this species is characterized by its great length and by the narrowness of its propatagium.

The carpal remex is not present, but its coverts are. They are well developed and similar to the adjoining coverts of the first secondary. Their placement is like that of the other falconiforms.

There is no fifth alula quill, but the pollex bears a straight claw 6.0 mm. in length.

Although the tertials reach their greatest development in the middle of the series, the distal feathers of this series are enlarged in both *Pandion* and *Cathartes* more than in the Accipitridae or Falconidae.

## PANDIONIDAE

*Pandion haliaetus carolinensis* (fig. 16).—The wing of the osprey is characterized by its great length and by the narrowness of the propatagium. In these respects and in others it resembles *Cathartes*. Since the propatagium is narrow there are fewer rows of lesser coverts than are present in the Accipitridae and Falconidae.



The carpal remex is well developed and is slightly smaller than the major upper secondary coverts. Its greater and middle upper coverts are of the same size as the adjoining ones belonging to the first secondary. The greater under carpal covert lies proximal to and between the greater and middle under coverts of the first primary, and is the same in size as the greater under covert of the first secondary.

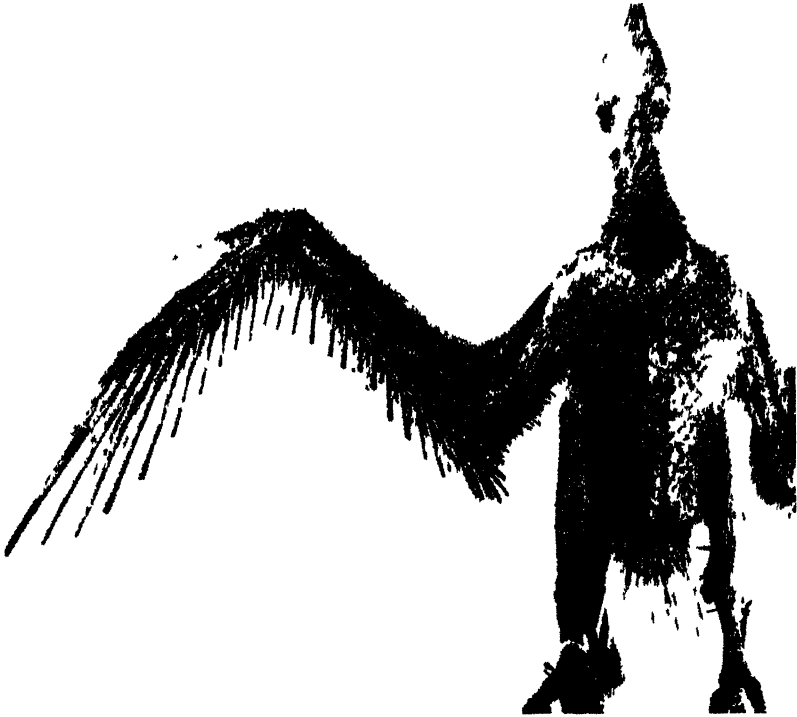


Fig. 16. Full ventral surface of *Pandion haliaetus carolinensis*. Figures 14, 15, and 16 illustrate the great elongation of the wing and the narrowness of the propatagium in *Pandion* and *Cathartes* as opposed to the short wing and wide propatagium in *Buteo*. The similarity of the trunk shape in *Cathartes* and *Pandion*, and the fusion of the thigh to the trunk in these two species, is also clearly shown.

The alula does not have a fifth quill, but the pollex does carry a straight claw 6.0 mm. in length. The upper and marginal alula coverts blend so completely that it is not practical to distinguish them. There are two under alula coverts.

## THE FEMORAL TRACT

### DEFINITIONS

The femoral tract covers the lateral surface of the thigh. Lateral extensions of the pelvic regions usually come near to or blend with the dorsal margin of this tract. The feathers occur in more or less clearly defined rows running diagonally across the long axis of the femur. Longitudinal rows running through the diagonal rows can also be seen.

### ACCIPITRIDAE

*Buteo jamaicensis borealis* (fig. 2).—This tract consists of six or seven diagonal rows of feathers. The rows from the lateral-pelvic region blend completely with the femoral tract at its dorsal margin. The feathers increase in size from the knee toward the trunk.

*Elanus leucurus majusculus* (fig. 3).—The femoral tract consists of only two longitudinal rows along the posterior margin of the thigh. The remainder of the thigh is covered with a large powder-down patch. This patch extends along the anterior margin of the thigh from a point above the knee to the margin of the sacrum, then posteriorly to the base of the uropygium and the posterior margin of the thigh.

*Ictinia mississippiensis* (fig. 4).—The femoral tract consists of five or six scattered feathers at the posterior margin of the base of the thigh. There are no other contour feathers on the lateral surface of the thigh, the greater part of this surface being covered with powder down. This patch of powder down covers about half the area that it does in *Elanus* and does not extend so far on the dorsal and posterior surfaces as it does in the latter species.

*Accipiter cooperii*.—This tract is the same as in *Buteo*, with the exception that there are fewer feathers in the vicinity of the knee.

*Circus cyaneus hudsonius*.—The femoral tract consists of two longitudinal rows of contour feathers extending along the posterior margin of the thigh. The lateral surface of the thigh is covered by a powder-down patch that is similar in extent to the one in *Ictinia*.

#### FALCONIDAE

*Falco mexicanus* (fig. 5).—This tract spreads over the lateral surface of the thigh and consists of approximately ten diagonal rows. Near the head of the femur the pelvic region blends with the femoral tract. The feathers reach their greatest development in the dorso-posterior area. The union of the femoral tract with the pelvic region is more complete than it is in the Accipitridae since the latter region extends farther laterally.

#### CATHARTIDAE

*Cathartes aura teter* (fig. 6).—This tract is similar in outline to the one in *Pandion*. It extends along the posterior margin of the thigh as approximately seven diagonal rows or three to four longitudinal rows.

#### PANDIONIDAE

*Pandion haliaetus carolinensis* (fig. 7).—This tract consists of about ten diagonal rows covering the area from the knee to the head of the femur and extending posteriorly to within a short distance of the uropygium. Usually the lateral extension of the pelvic region touches its dorsal margin. Its feathers increase in size as the tract progresses from the knee toward the trunk, and reach their greatest development on the dorsoposterior margin.

### THE CRURAL TRACT

#### DEFINITIONS

The crural tract covers the leg from the knee to the scutes of the tarsus. Its feathers are arranged in diagonal and vertical rows and are usually larger on the external than on the internal surface of the leg.

#### ACCIPITRIDAE

*Buteo jamaicensis borealis* (figs. 2, 8).—On the external and ventral surfaces there are numerous diagonal rows of large-shafted feathers, whereas on the internal surface there are not as many rows and the feathers are fewer and smaller. The feathers of the posterior half of the external surface form the "flag."

*Elanus leucurus majusculus* (figs. 3, 9).—This tract is essentially like that of *Buteo*.

*Ictinia mississippiensis* (figs. 4, 10).—The crural tract is like that of *Buteo*.

*Accipiter cooperii*.—This tract is like that of *Buteo* except that on the external surface there are fewer diagonal rows and the rows are spaced farther apart.

*Circus cyaneus hudsonius*.—The crural tract is similar to that of *Buteo* except that the rows on the dorsolateral surface are farther apart and are approximately at right angles to the long axis of the leg instead of diagonal to it.

## FALCONIDAE

*Falco mexicanus* (figs. 5, 11).—This tract differs from that of the Accipitridae in having only the feathers of the ventrolateral part of the external surface enlarged instead of having the greater part of the external surface covered with large feathers. These enlarged feathers form the flag.

## CATHARTIDAE

*Cathartes aura teter* (figs. 6, 12).—This tract extends from the knee to the unfeathered tarsus. The feathers are spaced widely apart in vertical and diagonal rows, and this spacing is similar to that occurring in the sternal region. All the crural feathers have large shafts, those of the dorsoexternal surface being the largest and those of the internal surface the smallest. There is no flag on the leg.

## PANDIONIDAE

*Pandion haliaetus carolinensis* (figs. 7, 13).—In the osprey the crural tract is a densely feathered area. The internal surface is more closely feathered than the external surface, but the feathers of the latter are heavier and longer. The feathers of both areas become slightly longer toward the distal end of the leg but not to the degree of producing the "flag" commonly found in hawks.

## DISCUSSION

From the preceding review it will readily be seen that the pterylosis is not at all uniform through the order Falconiformes; rather, that this order breaks up into three groups within each of which the basic plan is markedly constant. The pterylosis exhibited in these groups can be termed, respectively, the accipitrid, the falconid, and the cathartid types. A summary of the characters of each type follows.

Accipitrid type (figs. 2, 8).—Upper ocular apterium large. Submalar apterium present. Dorsal-cervical region narrow and lateral-cervical apteria wide. Dorsal region consists of one row of feathers on each side of median line. Pelvic region with one row of feathers directly upon median line, and with one or more rows parallel with and on each side of this median one. One or more rows extend diagonally out from anterior portion of pelvic region toward head of femur. Calami of rectrices enclosed in a patagium. Femoral tract consists of diagonal rows extending over entire lateral surface of thigh. Sternal and axillar regions narrow and joined in their anterior portions but separated posteriorly. Abdominal region narrow and ends far anterior to anus. Subaxillar region separated from axillar region. Humeral tract narrow and closely feathered. Lateral-cervical patagium (parapatagium) large. Anterior-humeral patagium (propatagium) wide. Alula quills five in number, the fifth vestigial. No claw on pollex.

Falconid type (figs. 5, 11).—Upper ocular apterium large. Submalar apterium present. Dorsal-cervical region narrow and lateral-cervical apteria wide. Dorsal and pelvic regions continuous and consist of a closely feathered band on each side and well away from the median line. A row of feathers on the median line in pelvic region. Calami of rectrices enclosed in a patagium. Femoral tract consists of diagonal rows extending over lateral surface of thigh but with the largest feathers in median portion of the tract. Sternal and axillar regions narrow and not joined in their anterior portions. Anterior portion of sternal region swings toward median line. Abdominal region narrow, its branches turning medially so that they almost join at anterior margin of anus. Subaxillar region separated from axillar region. Humeral tract narrow and closely feathered. Lateral-cervical patagium well developed. Anterior-humeral patagium wide. Alula quills five in number, the fifth vestigial. Curved claw on pollex.

Cathartid type (figs. 6, 12).—Upper ocular apterium narrow. Submalar apterium absent. Dorsal-cervical region wide and lateral-cervical apteria narrow. Dorsal and pelvic regions continuous and consist of a wide area on each side of median line. No row of feathers on

median line of pelvic region. Calami of rectrices not enclosed in a patagium but inserted directly in body of uropygium. Femoral tract consists mainly of two or three longitudinal rows along posterior margin of thigh. Sternal, axillar, and subaxillar regions fused and extend over whole of breast surface except for narrow apterium on median line. Abdominal region is narrowed extension of sternal region and ends anterior to anus. Humeral tract wide and its feathers set far apart. Lateral-cervical patagium small, only present at junction of neck and trunk. Anterior-humeral patagium narrow. Alula quills four in number. Straight claw on pollex.

Hawks having the accipitrid type of pterylosis were found in the subfamilies Elaninae, Perninae, Milvinae, Accipitrinae, Buteoninae, Aegypiinae, Circinae, and Circaetinae. All these are currently considered subfamilies of the Accipitridae. The family Sagittariidae also exhibits, at least in the pelvic region, characters similar to those of the accipitrid pterylosis. The osprey, the special subject of this study, was found to have a type of pterylosis (figs. 7, 13) entirely different from any occurring in the family Accipitridae, with which *Pandion* is usually placed.

The falconid type of pterylosis was found in the subfamilies Herpetotheriinae, Polyborinae, and Falconinae, all of the family Falconidae.

The cathartid type of pterylosis occurred in *Cathartes aura* and *Pandion haliaetus*.

From the foregoing evidence it appears that pterylosis is a feature of appreciable taxonomic importance. All hawks exhibiting the accipitrid type have previously been segregated in a single group based upon characters other than those pertaining to pterylosis. This same statement is true with respect to the falconid type and, so far as the Cathartidae are concerned, with the cathartid type. It is therefore apparent that, within the order Falconiformes, similarity of pterylosis indicates close relationship.

The question now arises: What is the significance of the similarity of the feather tracts between *Pandion* and *Cathartes*? I propose to demonstrate that, again, this is one of relationship.

As can be gathered from the detailed description of these two species, the general outlines of the feather tracts, especially those of the trunk, are alike. All the characters given for the cathartid type apply equally as well to *Pandion* as to *Cathartes*. In the possession of most of these characters they differ greatly from either the Accipitridae or the Falconidae. The main differences between the feather tracts of *Pandion* and *Cathartes* are those which would appear to have been brought about by modifications in the osprey to withstand frequent submersion. These adaptations have taken the form of a widening of certain of the tracts and an increase in the number of feathers within these tracts and have occurred mainly upon the neck, legs, and ventral surface of the trunk. On the dorsal surface, where there has been little need for adaptive modification, there is less difference between the tracts of the two species.

Since adaptive modification within the feather tracts of the osprey has taken the form of an increased number of feathers and a widening of the tracts, rather than a loss of feathers or reduction in size of the tracts, the absence of a median row of feathers in the pelvic region is indicative that the pterylosis of *Pandion* is not a modification of either the falconid or the accipi-

trid type. The alternative which I adopt is that the pterylosis of *Pandion* represents a modification of the cathartid type and that the resemblance indicates a positive relationship between the osprey and the New World vultures.

This relationship between the osprey and the Cathartidae is shown not only in the pterylosis but also in many other anatomical characters. Except for the plantar tendons I make no attempt here to demonstrate these; but a few examples may be cited. In both *Pandion* and *Cathartes* the thigh is attached throughout its length to the trunk and is but slightly movable, whereas in all other hawks it is attached only at its proximal end and moves freely. The general proportions and shape of the trunk are the same in these two forms but trenchantly different from those of other falconiforms. The Cathartidae and *Pandion* are the only forms in which the orbital process of the lacrimal is missing.

### THE PLANTAR TENDONS

At one time much taxonomic importance was placed upon the arrangement of the plantar tendons, but they have come to be looked upon by some writers as misleading when applied to taxonomy. It is possibly true that this application has been carried too far, but it is probable that many of the misinterpretations have resulted from lack of material and from inaccurate data. Although similarity may be only coincidence it may also indicate relationships, and when similarity of plantar tendons occurs along with agreement of other characters it can be interpreted as substantiating evidence.

In the following descriptions of the arrangement of the plantar tendons in the falconiforms, "tendon P" refers to the tendon for the flexor hallucis longus muscle and "tendon A" to the tendon for the flexor perforans digitorum profundus muscle.

*Buteo swainsoni* (fig. 17a).—At the ankle joint, tendon P lies on top of tendon A. Both are free throughout the greater length of the tarsometatarsus but are joined by a thin viniculum in their lower third. Tendon P supplies digit 1 and sends a branch to digit 2. Tendon A supplies digits 2, 3, and 4.

*Falco mexicanus*.—The plantar tendons present the same arrangement as in *Buteo* except that the viniculum joins them throughout more of their lengths. The viniculum starts shortly after the tendons pass the heel and extends to the point where they branch.

This arrangement of the tendons in *Buteo* and *Falco* agrees with the one described by Seebohm (1890, p. 201), who found it to exist in nine genera of the Falconiformes. Since it is the one that occurs in the superfamily Falconoidea it may be known as the falconoid type.

*Cathartes aura teter* (fig. 17b, c, d).—The two plantar tendons are parallel at the ankle joint, not superimposed as in *Buteo*. About the middle of the tarsometatarsus, they come together and fuse. In the proximal part of this fusion, tendon A partly surrounds tendon P. Both tendons send fibers to all four toes. This condition is different from that given by Seebohm (1890, p. 203), who describes tendon A as going to digits 1, 2, and 3, and tendon P as leading to 2, 3, and 4. This arrangement of the plantar tendons may be known as the cathartid type.

*Pandion haliaetus carolinensis* (fig. 17e, f).—At the ankle joint, tendon P does not completely cover tendon A but overlaps about half of it. Halfway down the tarsometatarsus the two tendons fuse and are greatly compressed laterally, resulting in a round tendon mass instead of a flat one as in *Cathartes*. Both tendons send fibers to all four toes. This is a distribution different from that ascribed to this species by Seebohm (1890, p. 201), who stated that tendon P extends to digits 1, 2, 3, and 4, whereas tendon A serves 2, 3, and 4.

From the foregoing description it can be seen that the distribution of the plantar tendons is the same in *Pandion* and *Cathartes* and that these two genera present a type of tendon distribution fundamentally different from that found in the other falconiforms. This fact I interpret as further evidence of the relationship of *Pandion* to the Cathartidae.

In the examination of these tendons some difficulty was had in the attempt

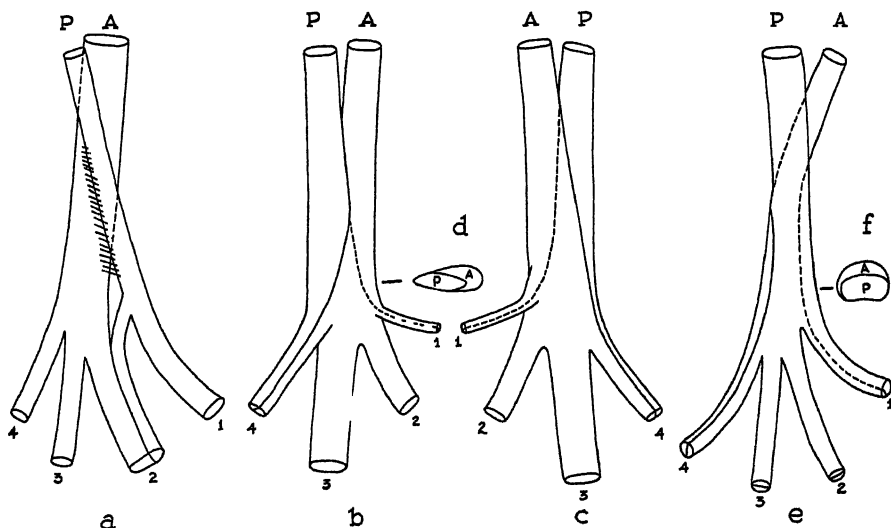


Fig. 17. Diagrammatic drawing of the plantar tendons of the left leg. a. *Buteo swainsoni*, posterior view. b, c, d. *Cathartes aura teter*, posterior, anterior, and sectional views. e, f. *Pandion haliaetus carolinensis*, posterior and sectional views.

to determine which toes were supplied by each tendon. In *Pandion* and *Cathartes* the two tendons are so thoroughly fused that any attempt to tear the two apart only leads to destruction, but it was discovered that by gently pounding the slightly dry tendon mass the fibers could be so loosened that they could easily be traced upward from each toe to the tendon from which they originated.

## CONCLUSIONS

Within the order Falconiformes the arrangement of the feather tracts supplies characters of definite taxonomic value. By the use of these characters the order can be divided into three natural groups which are, except for the inclusion of the osprey, equivalent to groups which have heretofore been established upon other evidence. The secretary bird may represent a fourth group although it is apparently more closely related to the Accipitridae than to any of the other falconiforms. The relationship of the osprey is shown by its pterylosis to be with the suborder Cathartae and not with the suborder Falcones, with which it has heretofore been placed. The osprey, in my final judgment, belongs to the family Pandionidae, equivalent in rank to the family Cathartidae, within the suborder Cathartae.

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**GEOGRAPHICAL VARIATION IN  
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**BY**

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# GEOGRAPHICAL VARIATION IN WOOD RATS OF THE SPECIES *NEOTOMA FUSCIPES*

BY  
EMMET T. HOOPER

(Contribution from the University of California Museum of Vertebrate Zoology)

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## INTRODUCTION

THE WOOD RATS, genus *Neotoma*, comprise a distinct group of ericetid rodents belonging to the subfamily Neotominae Merriam (1894b:225-252). This genus is restricted in its occurrence to North America southward to Nicaragua. The greater number of the species occur in the more arid and physiographically diverse western half of the continent.

The species *Neotoma fuscipes* is endemic to the Pacific coastal area of the United States and Lower California. The number of individuals, as well as the number of the subspecies in this species, exceeds that of any other species of the genus found within the area, a fact which may be accepted as evidence that *N. fuscipes* successfully meets the requirements of its environment. From close to the Columbia River its range extends southward to include the Sierra San Pedro Mártir of northern Lower California. At the south its range reaches approximately 30 degrees north latitude; it is bounded on the east, in general, by the Cascade-Sierra Nevada mountain system and the Mohave and Colorado deserts. Altitudinally, it extends from near sea level along the Pacific Ocean up to nearly 9000 feet farthest south, on the Sierra San Pedro Mártir.

The zonal range is comparatively wide. Specimens of certain subspecies have been taken from areas as low as the Lower Sonoran and as high as the Canadian. However, the species as a whole reaches its peak of population in the Upper Sonoran zone, and, for this reason, by some students has been termed an "indicator" of this zone.

Goldman (1910:86), considering the *fuscipes* "series" of wood rats to be markedly distinct from all other North American wood rats, created for it the subgenus *Homodontomys*. Subsequent authors have pointed out that some individuals in *fuscipes* are intermediate between typical specimens of *Neotoma* (subgenus) and *Homodontomys*, and have intimated that the latter subgenus is therefore too unstably based to be of real taxonomic use. A decision on this question is outside the scope of the present paper. Suffice it to say that the structural features considered by Goldman to be diagnostic of *Homodontomys* have been useful in distinguishing the species *fuscipes* from the three other species of wood rats which inhabit the area along the Pacific Coast. These features are, to quote from Goldman (*loc. cit.*): "Maxillary tooth row only slightly narrower posteriorly than anteriorly; third upper molar broad and heavy, with middle enamel loop partially or completely divided by deepening of inner reentrant angle [so that there are four more or less complete enamel loops]; frontals constricted near middle; bullae large; tail terete,

tapering and short-haired; hind foot naked below along outer side, at least to tarso-metatarsal joint."

My studies with the species *N. fuscipes* indicate that there is adequate basis for recognizing eleven subspecies, five more than Goldman (1910) recognized. These are as follows: *N. f. monochroura* Rhoads; *N. f. fuscipes* Baird; *N. f. annectens* Elliot; *N. f. riparia*, new subspecies; *N. f. perplexa*, new subspecies; *N. f. bullator*, new subspecies; *N. f. streatori* Merriam; *N. f. simplex* True; *N. f. luciana*, new subspecies; *N. f. macrotis* Thomas; and *N. f. martirensis* Orr.

On the basis of certain conspicuous *adult cranial* characters, these eleven subspecies can be segregated into three groups as follows:

*Group A.*—Narrow, long interpterygoid fossa; posterior outline of palatal bridge concave; palatal bridge appearing about equal to length of incisive foramen; total lengths of foramen and bridge, minimum, 18.5 mm. in females; auditory bullae moderately large. Subspecies included: *monochroura* and *fuscipes*.

*Group B.*—Narrow, long interpterygoid fossa; posterior outline of palatal bridge convex, often prolonged into a heavy, median projection; palatal bridge appearing about equal to length of incisive foramen; total lengths of foramen and bridge, minimum, 18.9 mm. in females (except 18.0 mm. in *perplexa*); auditory bullae large. Subspecies included: *annectens*, *riparia*, *perplexa*, and *bullator*.

*Group C.*—Interpterygoid fossa wide and spatulate (averaging narrower in *streatori*); posterior outline of palatal bridge most often concave; palatal bridge appearing much shorter than incisive foramen; total lengths of foramen and bridge, maximum, 18.7 mm. in females; auditory bullae small. Subspecies included: *streatori*, *simplex*, *luciana*, *macrotis*, and *martirensis*.

The three geographic areas now occupied by the three groups of *Neotoma fuscipes* (above indicated) show a notable correspondence with the areas of occurrence of the three principal floral elements or associations of the region (see Mason, 1936:188–189). Group A occurs, for the most part, with the floral element which is thought to have migrated from Alaska southward into California, where it divided, one section of it following the Coast Range and the other the Sierra Nevada. Group B of *N. fuscipes* occurs along with the floral element confined to and thought to have originated (as a distinct floral unit) probably in west-central California, an insular area during Pliocene time (Reed, 1933:252). Group C occurs mostly in territory supporting the floral element thought to have progressed northward from the Mexican Plateau region. It is possible that the particular environmental factors which now limit the distribution of each floral element also now restrict the range of each group of *N. fuscipes*.

The areas of occurrence of the several subspecies of *Neotoma fuscipes* are strikingly similar to those of the subspecies of *Sylvilagus bachmani* (Orr, MS). A boundary which defines the range of a subspecies of *N. fuscipes* also limits the range of a race of *S. bachmani*. In each species, subspecific intergradation occurs in geographically comparable areas.

The species *N. fuscipes* is commonly considered to be a form restricted to the chaparral belt. However, in some areas it occurs where chaparral is either not abundant or is even absent. For example, *N. f. riparia* along the San Joaquin River has access to no true chaparral and lives almost entirely among the branches of trees, including buttonwillow (*Cephalanthus*), ash (*Fraxinus*), and, especially, oak (*Quercus*). Indeed, as a general rule, the wood rats occur in regions where oaks as well as chaparral occur, and the distribution of each subspecies conforms closely with the distribution of one or more species of oaks (Ritter, MS). The possibility of a causal relationship here cannot be ignored, though to me it seems probable that some third factor accounts for the similar occurrence of oaks and wood rats, rather than that the oaks themselves determine the occurrence of the rats.

Several kinds of barriers appear to be effective at the present time in limiting the ranges of the subspecies of *N. fuscipes*. Bodies of water are barriers. The most obvious barrier toward the west is the Pacific Ocean. No *fuscipes* wood rats have been taken from any of the coastal islands. San Francisco Bay separates groups A and B, allowing no intergradation. The Columbia River marks the northern limit of the *fuscipes* rats and may be an ultimate barrier to distribution.

Temperature appears to be only secondarily important as a barrier to any subspecies of *N. fuscipes*. Each geographic race except *riparia* more or less completely spans two or three life zones, thus perhaps evidencing a relatively wide range of tolerance for temperature. Even so, extremes of temperature are probably effective in limiting distribution, for the species *fuscipes* is not found in the cold alpine regions or out on the hot, dry desert proper. However, it should be pointed out that their absence in those regions may be due directly to the lack there of the necessary vegetation or of some other critical factor or factors for wood-rat existence, rather than to temperature *per se*.

Humidity, whether relative humidity of the air, or rainfall, may play a part in limiting the ranges of the subspecies. The races inhabiting the humid coastal area are darkest in color, those of the relatively less humid Sierra Nevada lighter, and those of the dry desert slopes most pallid, with least black pigment over all parts of the pelage.

#### MATERIALS AND ACKNOWLEDGMENTS

One thousand and fifty-nine of the specimens used in this study are to be found in the Museum of Vertebrate Zoölogy. The remaining 125 are in the following collections: Bureau of Biological Survey, United States Department of Agriculture; Fresno State College; private collections of Professor William T. Shaw, O. P. Silliman, Jack C. von Bloeker, Jr., John R. Arnold, and William B. Richardson.

For use of the materials studied, the author thanks Dr. Hartley H. T. Jackson, Custodian of the Biological Survey Mammal Collection; Professor A. E. Culbertson, Fresno State College; and the owners of the above-mentioned private collections. To Professor Joseph Grinnell and E. Raymond Hall the writer is indebted for assistance with the present study.

## MEASUREMENTS AND METHODS

Measurements of total length, tail vertebrae, and hind foot are those recorded by the collector. All other measurements were taken by the writer himself; all averages were determined and all percentages (proportions) were computed by him. All measurements are given in millimeters and tenths of millimeters, and, with a few exceptions, were taken in accordance with current custom. The exceptions require descriptions as follows:

*Ear from anterior notch.*—Inside of ear, from anterior notch near base of ear to the topmost point on rim of pinna, when ear is extended; measured on dry skin.

*Length of nasals.*—Greatest length of a nasal, parallel to the long axis of the skull.

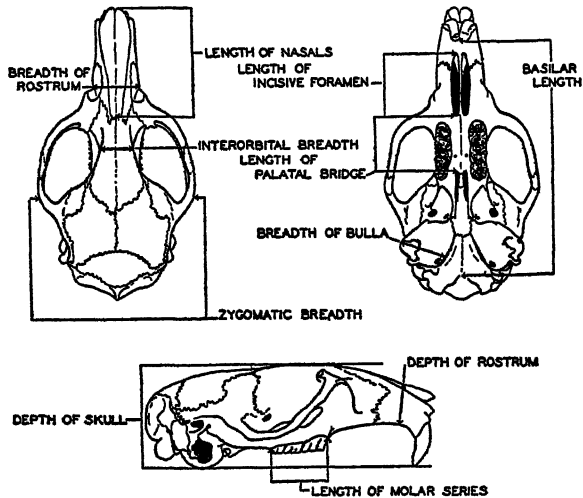


Fig. 1. Three views of skull of *Neotoma fuscipes annectens*, labeled to show methods of measuring here employed.

*Depth of skull.*—Greatest depth of skull, from highest point on dorsal surface (along midline) to plane touching the ventromost tips of incisors and auditory bullae (taken with skull resting on glass slide; depth of slide subtracted from resulting measurement).

*Breadth of rostrum.*—Greatest breadth across rostrum, on a plane just anterior to the ascending branches of the maxillae at the infraorbital foramina.

*Depth of rostrum.*—Taken at a tangent to the dorsoventral axis of the skull, from the anterior borders of the incisive foramina, dorsally to the most depressed part of the upper surface of the nasals.

*Length of incisive foramen.*—Greatest length of anterior palatal foramen, from postero-most inner border to anteromost inner border.

*Length of palatal bridge.*—Least length of hard palate; taken parallel to the long axis and on the same side of the median line as the incisive foramen measured.

*Length of upper molar series.*—From anteromost point on alveolar border of  $M^1$  to posteromost alveolar border of  $M^3$ .

*Breadth of bulla.*—Breadth on external surface of bulla from anterosuperior border of meatus to a point on the medial surface of the bulla at right angles to long axis of bulla.

Throughout this study, in the measurement and description of skulls, those from medium-aged animals were used whenever such were available. Skulls measured and described as typical of each race were always from animals of

medium age, as exhibited by the following adult characters: sutures well closed; a moderate amount of angular ridging of cranium, particularly of lambdoidal crest and of frontals in the interorbital region; last upper molars with exterior bases of reëntrant angles visible; teeth showing moderate degree of wear.

Although study skins in series of several of the geographic races show marked color differences in mass effect, at the same time the fundamental color may be almost identical in each series. To convey an appreciation of these differences taxes the skill of the describer. In all the races of *Neotoma fuscipes* the color tone is cinnamon, with variations toward tints of buff and pink. The mass effect of the color depends on the width of the subterminal, cinnamon-pigmented bands of the hairs, on the relative number of black hairs present, and on the amount removed, by wear, of the black tipping—with corresponding exposure of the subapical, lighter bands. In the attempt to define the dorsal coloration of the tail, and, in some specimens, the feet, it proved so difficult to designate one or more colors from a standard key as *the* color reflected that it was deemed advisable to resort to such vague terms as "dark," "dusky," "dark brown," and "light." The color names which begin with capital letters are those taken from Ridgway's Color Standards and Color Nomenclature (1912) upon direct comparison of the study skins with the color plates in that work. Descriptions of coloration are from adult animals in adult summer pelage (except in two races when only specimens in winter pelage were available). The summer pelage is ordinarily the pelage acquired at the annual molt in the fall, and it therefore has been subjected to many months of wear and fading. However, obviously "burnt" or badly worn specimens were not used.

In the lists under "Specimens Examined," localities of occurrence are arranged alphabetically, first by counties, and then under each county by the initial letter of the first capitalized word.

#### *Neotoma fuscipes monochrourea* Rhoads

##### Rhoads Wood Rat

*Neotoma monochrourea* Rhoads (1894:67-68).

*Neotoma fuscipes* Baird (1857:495-496), part.

*Neotoma splendens* True (1894:353). Type from [Nicasio] Marin County, California.

*Neotoma fuscipes monochrourea*, Stephens (1906:116).

Type.—Adult male; no. 1739, Acad. Nat. Sci. Phila.; Grants Pass, Josephine County, Oregon; collected by George [H.] Kenzer [sometime prior to September, 1893 (see under "Remarks")] (after Rhoads, 1894:67-68).

Range.—Coastal belt of Oregon and California; west of Cascade and Coast ranges, south from Columbia River to San Francisco Bay. Vertical range from near sea level to 4700 feet (on Horse Mountain, Humboldt County). Zonal range chiefly Transition, but extending from Lower Sonoran to Canadian.

Diagnosis.—Size: large; tail long; ear medium in length (see under "Measurements"). Color: dark Cinnamon to Pinkish Cinnamon above; tail dark brown, usually unicolorous; hind feet dusky, usually to toes. Skull: large and angular; rostrum long and deep; incisive foramina long and moderately narrow; palatal bridge about equal to length of upper-molar row and approximately 85 per cent of length of incisive foramen; bullae medium in size, not reaching to within 1 mm. of foramen ovale.



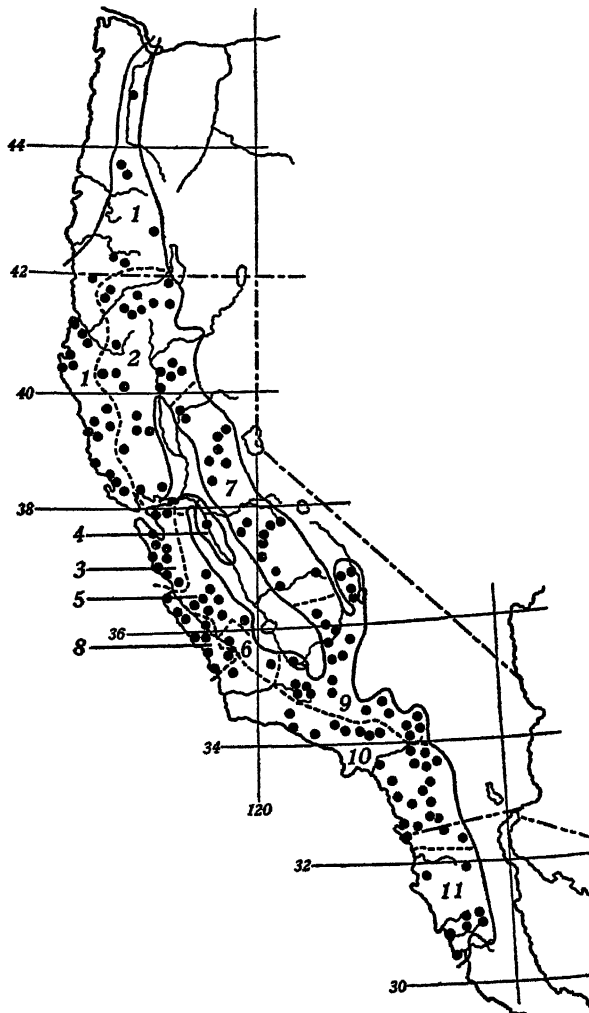


Fig. 2. Map showing the distribution of the subspecies of *Neotoma fuscipes*, as established by specimens examined by the author. 1, *N. f. monochrourea*; 2, *N. f. fuscipes*; 3, *N. f. annectens*; 4, *N. f. riparia*; 5, *N. f. perplexa*; 6, *N. f. bullator*; 7, *N. f. streator*; 8, *N. f. luciana*; 9, *N. f. simplex*; 10, *N. f. macrotis*; 11, *N. f. martirensis*.

*Color*.—Cinnamon to Pinkish Cinnamon above, appearing darker because of presence of numerous black and black-tipped hairs; purer cinnamon on sides (black pigment not predominant); throat, chest, and inguinal region white throughout; hairs of belly plumbeous at base and most often light cinnamon at tips; tail typically unicolorous, dark cinnamon brown (sometimes lighter below than above); dorsal sides of forefeet white throughout to toes, or lightly clouded with dusky; hind feet dusky, usually to toes; toes of fore and hind feet white.

*Skull*.—Large and angular; rostrum long, deep, and relatively narrow; zygomata heavy and wide spreading; incisive foramina long and narrow; length of palatal bridge about

equal to length of upper-molar series and approximately 85 per cent of length of incisive foramen; interpterygoid fossa long and narrow (width at antermost end about equal to alveolar breadth of  $M^2$ ; outline of palatal bridge at posterior border concave or slightly emarginate; bullae medium in size (smaller than in *riparia*, *bullator*, and *annectens*, but about equal to those in *fuscipes*) and antermost part of inflated part more than 1 mm. posterior to foramen ovale; anterosuperior border of meatus projecting moderately (less than in *annectens*, *riparia*, and *bullator*).

*Comparisons.*—Except for the smaller ear, *monochroura* is indistinguishable in external characters from *annectens*, but differs in the following well-defined cranial characters: interpterygoid fossa averaging slightly wider, at antermost border about equal to alveolar breadth of  $M^2$  (generally less than breadth of  $M^2$  in *annectens*); posterior outline of palatal bridge concave or emarginate; bullae smaller, with anterosuperior border of meatus projecting more strongly. From *fuscipes*, it differs in its much darker, more pinkish cinnamon dorsal coloration, greater amount of ventral pigmentation, more extensive dusky area of hind feet, unicolorous (rather than bicolorous) tail, and length of palatal bridge averaging nearer length of incisive foramen.

*Remarks.*—In the present study type specimens and topotypes were ignored as such and were used only in the same way as other specimens, until the number of subspecies, and the geographic range of each, was determined. Only then were type specimens and topotypes given special study, as a means of allocating previously proposed names. As might be expected, specimens from certain type localities were found to be intermediate in characters between two geographical races.

Such a problem was met in the determination of the status of the wood rats inhabiting the area north of San Francisco Bay and east of the Sacramento River. A lighter, more buffy inner Coast Range-Sacramento Valley form seemed sufficiently distinct from the darker, more cinnamon-colored coast form to warrant subspecific recognition. However, specimens at hand from  $1\frac{1}{2}$  miles south of Petaluma, Sonoma County, the type locality of *N. f. fuscipes*, although typical of neither the coast nor the valley forms, show greater affinity with the latter. Because the differential features involved are mainly ones of color, an examination of the type specimen, now a skeleton in the National Museum (Lyon and Osgood, 1909:99), would not be expected to aid in more definitely allocating the name *fuscipes*.

If the subspecific name *fuscipes* be applied to the inland form, one of two other names proposed by authors subsequent to Baird (1857) become available to designate the coastal race. The name *N. monochroura* Rhoads (1894), which appeared in print before *N. splendens* True (1894), is thus raised from synonymy. Specimens available for comparison from Grants Pass, Oregon, the type locality of *monochroura*, and other near-by localities in the Rogue River Valley are intermediate in color between the two races, but appear to me to be closer to the coast form, *monochroura*. Specimens from Marin County, California, the type locality of *N. splendens*, are typical of the coastal form, exhibiting the dark pinkish cinnamon coloration characteristic of that race. If True (1894) compared a series from Marin County with one from Petaluma, the type locality of the inland race, he was justified in designating *splendens* as distinct.

Along the eastern border of its range, *monochroura* grades toward *fuscipes*.

At the south, San Francisco Bay prevents intergradation with *annectens*. Specimens progressively farther inland from the humid fog belt become lighter dorsally, have less ventral pigmentation, lighter hind feet, and tail lighter below than above. However, these modifications are chiefly local in geographical extent and may be considered within the limits of variation of the race. Specimens from the vicinity of South Fork Mountain, near the Humboldt-Trinity county line, are intermediate in character between *fuscipes* and *monochrourea* and might easily be referred to either race. In this study they are identified as *fuscipes*.

Wharton Huber, Associate Curator of Mammals, Academy of Natural Sciences of Philadelphia, informs me under date of January 28, 1936, that the type specimen of *N. f. monochrourea* "was received through exchange with the Wagner Institute of Philadelphia in 1894. It was an old mounted specimen at the time and was relaxed and unmounted, the skull taken out, probably by Rhoads himself." A letter, dated February 10, 1936, from Carl Boyer, Director of the Wagner Free Institute of Science, gives the following information: "There are two specimens in our collection, accession number 5145, marked 'duplicate types' NEOTOMA MONOCHROURA RHOADS, from Josephine County, Oregon. The date in the accession book is September, 1893, and the specimens were bought from George H. Kenzer." The type specimen was probably accessioned with the above-mentioned "duplicate types," and, thus, was collected by Kenzer at some time prior to September, 1893.

*Specimens examined*.—A total of 179 from the following localities: **Oregon:** *Douglas County:* Drain, 2 (U. S. Nat. Mus., Biol. Surv. Coll.); Elkhead, 1 (U. S. Nat. Mus., Biol. Surv. Coll.). *Marion County:* Salem, 2 (U. S. Nat. Mus., Biol. Surv. Coll.);  $3\frac{1}{2}$  mi. E Salem, 1 (Coll. J. C. von Bloeker, Jr.). *Jackson County:* Belmont Orchard, 6 mi. S Medford, 3;  $\frac{1}{2}$ -mi. S Belmont Orchard, 6 mi. S Medford, 2; between Jacksonville and Rush, 1; Prospect, 1. *Josephine County:* 1 mi. S Grants Pass, 1; 5 mi. W Grants Pass, 1. **California:** *Del Norte County:* East Fork Illinois River, 1900 ft.,  $\frac{1}{4}$ -mi. S Oregon line, 1. *Humboldt County:* Coyote Peak, 3000 ft., 4; Cuddeback, 10; Eureka, 1; Fair Oaks, 3; Ferndale, 15; Horse Mountain, 4700 ft., 10. *Marin County:* Inverness, 1; 4 mi. W Inverness, 300 ft., 1 (Coll. J. C. von Bloeker, Jr.); 3 mi. W Inverness, 200–400 ft., 17; Lagunitas, 1; Mailliard, 1; Mount Wittenberg, 1000 ft., 2 mi. W Olema, 1; Nicasio, 6. *Mendocino County:* Albion River,  $\frac{1}{2}$ -mi. W McKays Gulch, 1; 3 mi. S Covelo, 12; Gualala, 14; Lake Leonard, 10 mi. NW Ukiah, 1; Lierly's Ranch, 2340 ft., 4 mi. S Mount Sanhedrin, 2; Mendocino City, 6; 3 mi. W summit Mount Sanhedrin, 10; Sherwood, 2; 6 mi. N Willits, 1400 ft., 1. *Sonoma County:* 7 mi. W Cazadero, 900 ft., 20; Freestone, 300 ft., 15; 1 mi. W Guerneville, 7; Smith Creek, near Monte Rio, 1.

***Neotoma fuscipes fuscipes* Baird**  
Sacramento Valley Wood Rat

*Neotoma fuscipes* (Cooper, MS) Baird (1857:495–496).

*Neotoma fuscipes fuscipes*, Goldman (1910:87–89).

*Types*.—Male; no. 2679, U. S. Nat. Mus.; Petaluma, Sonoma County, California; collected February, 1856, by E. Samuels (after Baird, 1857:495–496). [Original specimen in alcohol, no. 2679, now prepared as a skeleton, no. 22026, Division of Comparative Anatomy, U. S. Nat. Mus. (Lyon and Osgood, 1909:99).]

*Range*.—Inner Coast Range of California, north from San Francisco Bay to Oregon line; at north, westward to Siskiyou Mountains and eastward through Siskiyou County at least

to Crescent Butte (3 miles west of Modoc County line) and through Shasta County as far as Haydenhill, Lassen County (Goldman, 1910). Vertical range from approximately 800 feet, near Petaluma, Sonoma County, to 5500 feet on Horse Ridge, southeast of Ruth, Trinity County. Zonal range Lower Sonoran into Transition.

*Diagnosis*.—Size: large (see under "Measurements"). Color: lighter and more buffy than *monochrourea* dorsally; white throughout ventrally; tail distinctly bicolored; dorsal sides of hind feet white throughout, or dusky only  $\pm$  1 cm. below ankles. Skull: essentially as in *monochrourea*, but with palatal bridge averaging shorter and interpterygoid fossa averaging longer.

*Color*.—Dorsal coloration Pinkish Cinnamon to Cinnamon-Buff, appearing much lighter than *monochrourea* from coastal region because of fewer black and black-tipped hairs; ventral color white throughout; fore and hind feet white, the dusky area of legs extending only  $\pm$  1 cm. on tarsi and never as extensive as in *monochrourea*; tail bicolored, dark brown above and white below.

*Skull*.—Similar to that of *monochrourea*, but with interpterygoid fossa averaging longer and palatal bridge averaging shorter. Many single skulls indistinguishable from *monochrourea*.

*Comparisons*.—The race *fuscipes* resembles closely the race *monochrourea*, but is distinguishable from it in the following well-defined pelage characters: dorsal coloration lighter and more buffy; ventral region white throughout; hind feet white; tail distinctly bicolored. From *simplex*, the race of group C which it resembles most closely, it differs in characters as follows: larger size; less grayish and more buffy coloration dorsally; lack of pigmentation ventrally; longer rostrum; longer palatal bridge (more than 8.4 mm. in specimens examined, but not so long as in *monochrourea*); larger bullae; and longer, narrower interpterygoid fossa.

*Remarks*.—*N. f. fuscipes* is a pale race interposed between the darker coastal and Sierran forms and intergrading with them along much of the periphery of its range. Along the western border, specimens from certain localities are intermediate in color characters between *fuscipes* and *monochrourea*. These localities follow: Petaluma, Sonoma County; region of South Fork Mountain and Mad River at the Humboldt-Trinity county line; Helena, Trinity County; Seiad Valley and Clear Creek, Siskiyou County, all in California; and localities in southern Rogue River Valley, Oregon. Specimens from these places are referred to *fuscipes*. In the intergrading area in Lassen County, east of the Sacramento River, some specimens have a darker, richer cinnamon color dorsally, a unicolored tail, and feet clouded with dusky to toes, extremes of variation not expressed elsewhere by either *fuscipes* or *streatorii*. In shorter rostrum and smaller bullae, these specimens resemble *streatorii*; however, in narrower interpterygoid fossa, longer palatal bridge, greater total length of foramen and bridge, and larger size, they are more like *fuscipes*. On the basis of affinity of a greater number of characters, they also have been referred to *fuscipes*.

*Specimens examined*.—A total of 127 from the following localities in California: *Colusa County*: Sites, 1; 3 mi. W Stonyford, 800 ft., 4. *Glenn County*: Winslow, 5 mi. W Fruto, 700 ft., 11. *Lake County*: K3 Lodge, Stubbs, 1. *Shasta County*: McCloud River, near Baird Station, 2; 12 mi. N North Yolla Bolly Mountain, 4000 ft., 2; Tower House, 1268 ft., 3. *Solano County*: 3 mi. W Vacaville, 700 ft., 7. *Sonoma County*: 1½ mi. S Petaluma, 8. *Siskiyou County*: Caves, 11 mi. NE Weed, 3600 ft., 1; Clear Creek, 1400 ft., 3 mi. W Klamath River, 5; Crescent Butte, 4500 ft. (approximately), Lava Beds National Monument, 7; Kangaroo Creek, 2; Parks Creek, 2900 ft., 1½ mi. SW Edgewood, 5; Picard, 4600 ft., 8 (U. S. Nat. Mus., Biol. Surv. Coll.); Scott River, 6 mi. NW Callahan, 6; Seiad Valley,

1400 ft., 1; 5.2 mi. E Tennant, 1; vicinity of Weed, 6. *Tehama County*: Middle Ridge, 3500 ft., 3 mi. N Mount Tomhead, 1; Saddle Camp Ranger Station, 3600 ft., Mount Tomhead, 1; vicinity of Mount Tomhead, 1. *Trinity County*: Helena, 1405 ft., 8; Horse Ridge, 5500 ft., SE Ruth, 4; Mad River ford, above Ruth, 2700 ft., 10; 3 mi. NNW Mad River bridge, South Fork Mountain, 2900 ft., 6; 1½ mi. N Mad River bridge, 3200 ft., South Fork Mountain, 2; 1 mi. NW Mad River bridge, 2300 ft., 1; Reilley's Ranch, 3000 ft., South Fork Mountain, 1; 1 mi. N Reilley's Ranch, 3700 ft., South Fork Mountain, 3. *Yolo County*: Rumsey, 500 ft., 13.

***Neotoma fuscipes annectens* Elliot**  
Portola Wood Rat

*Neotoma fuscipes annectens* Elliot (1898:201-202).

*Neotoma fuscipes* Baird (1857:495-496), part.

*Neotoma fuscipes affinis* Elliot (1898:202-203). Type from Alum Rock Park, Santa Clara County, California.

*Type*.—Adult male; no. 2160, Field Mus. Nat. Hist.; Portola, San Mateo County, California; collected December 23, 1895, by [W. W.] Price and [D.] Coolidge (see Goldman, 1910:90).

*Range*.—Coastal region, entirely west of Diablo Range, south from San Francisco Bay to Monterey Bay. Vertical range from near sea level up at least to 3000 feet on Mount Diablo, Contra Costa County. Zonal range chiefly Transition, but into Upper Sonoran in certain regions.

*Diagnosis*.—Size: large (see under "Measurements"). Color: dark Pinkish Cinnamon dorsally; feet dusky. Skull: large; rostrum moderately long, wide, and deep; incisive foramina long and narrow; palatal bridge long (about equal to length of molar row and slightly shorter than length of incisive foramen); posterior border of palatal bridge convex, often with a heavy median projection.

*Color*.—Essentially the same as for *monochroua*.

*Skull*.—Long, narrow, and angular; similar in proportions to *monochroua*, but differing in the following structural characters: interpterygoid fossa narrower (width at anteromost border generally less than breadth of  $M^2$ ); palatal bridge convex in outline at posterior border, and most often prolonged into a heavy, median projection; bullae less inflated, and with anterosuperior border of meatus projecting more strongly.

*Comparisons*.—The characters distinguishing *annectens* from *monochroua* are given in the descriptions above. From *riparia*, *annectens* differs in the following: smaller size; darker, dorsal coloration; more ventral pigmentation; smaller ears; less angular zygomata; shorter, narrower, and shallower rostrum; smaller bullae (anteromost border of inflated part not reaching foramen ovale). It is distinguishable from *perplexa* by the larger size, darker color, dusky feet, smaller ears, proportionately smaller bullae, and deeper rostrum. From *bullator*, it differs in darker color, dusky feet, unicolored tail, much smaller ears, less inflated bullae, and narrower rostrum.

*Remarks*.—Specimens from various localities on the east side of San Francisco Bay grade toward *riparia* and *perplexa*, and are not typical of the race *annectens*. Specimens from Berkeley, Alameda County, resemble *annectens* in pelage characters, but in cranial characters are most like *riparia*. Specimens from Mount Diablo and near Walnut Creek vary appreciably in pelage characteristics. One available adult skin from this region exhibits the smaller size and reddish coloration characteristic of *perplexa*; another specimen has the larger ears and white feet characteristic of *riparia*. To the south, where the range of *annectens* meets that of *luciana*, intergradation occurs. Specimens from Strawberry Canyon (about 5 miles southeast of Watsonville), Monterey County, in cranial characters are quite typical (as herein defined).

of *annectens*. In no diagnostic character are they found to resemble *luciana*. However, farther southward the two forms do intergrade. For discussion of this, see account of *luciana*.

*Specimens examined*.—A total of 98 from the following localities in **California**: **Alameda County**: Arroyo Valle, 1; Berkeley, 18; Oakland, 1. **Contra Costa County**: W side Mount Diablo, 1750 ft., 7; 2 mi. SW Walnut Creek, 200 ft., 10. **Monterey County**: Strawberry Canyon, 200–500 ft., 11 (Coll. O. P. Silliman). **San Mateo County**: Alpine Creek Ranch, 1700 ft., 3; Corte Madera Creek, 1; La Honda, 6; Menlo Park, 5; Pescadero, 1; Portola, 4;  $\frac{3}{4}$ -mi. SW Portola, 3; Redwood City, 2. **Santa Clara County**: Black Mountain, 11; Los Gatos, 2; Stanford University, 2; Stevens Creek, 1. **Santa Cruz County**: Bear Creek Road, 2 mi. NE Boulder Creek, 650 ft., 5 (Coll. O. P. Silliman); Ben Lomond, 1; head of Doyle Gulch, 1; Granite Creek, 1 (Coll. J. C. von Bloeker, Jr.); San Lorenzo River, 1 mi. S Ben Lomond, 1.

***Neotoma fuscipes riparia*, new subspecies**  
**San Joaquin Valley Wood Rat**

*Neotoma fuscipes annectens*, Goldman (1910:90–91), part.

*Type*.—Adult male, skin and skull; no. 55130, Mus. Vert. Zoöl.; Kincaid's Ranch, 2 miles northeast of Vernalis, Stanislaus County, California; collected November 4, 1932, by R. T. Orr; original no. 861.

*Range*.—Known only from vicinity of type locality, but probably extending along west side of San Joaquin River south to southern Merced County or northern Fresno County and north to region of Suisun Straits, Contra Costa County. Zonal range Lower Sonoran and Upper Sonoran.

*Diagnosis*.—Size: large; ears and hind feet large (see under "Measurements"). Color: resembling *N. f. perplexa*, but with less reddish cinnamon dorsally. Skull: longer and more angular, rostrum longer, broader, and deeper, and incisors more procumbent, in comparison with *annectens* from San Mateo County; zygomata most widely spread and angular of all races of *fuscipes*; bullae large, but less inflated than those in *bullatior*; antermost border of inflated part of bulla reaching to within 0.7 mm. of foramen ovale.

*Color*.—Similar to *perplexa* dorsally and ventrally, but appearing more grayish and less cinnamon-colored above, because of narrower, subterminal, cinnamon-colored bands on hairs, and of presence of greater number of black or black-tipped hairs.

*Skull*.—Similar in general appearance to *annectens*, but distinct as follows: longer and deeper; rostrum longer, broader, and deeper; zygomata more spreading and angular; bullae larger; incisors more procumbent.

*Comparisons*.—Besides the above-mentioned cranial characters, *riparia* is distinguishable from *annectens* by external characters as follows: larger size; lighter, more grayish dorsal coloration; hind feet larger, and white, rather than dusky, above; tail distinctly bicolored, or at least lighter below than above; ears longer. From *perplexa*, *riparia* differs in its larger size and in having a more grayish (less reddish) dorsal coloration; more massive skull; longer, heavier rostrum; wider spreading and more angular zygomata; longer, narrower incisive foramina; and larger bullae (extending anteriorly to or within 0.7 mm. of foramen ovale). It can be readily distinguished from *bullatior* by its smaller ears; slightly darker, more reddish (rather than buffy) dorsal coloration; smaller, less inflated bullae; and wider spread of zygomata.

*Remarks*.—*N. f. riparia* is known only from the vicinity of the type locality. However, it probably ranges south, along the river bottom lands, as far as southern Merced County or northern Fresno County, since the same environmental conditions evidently prevail throughout this area. In the account of *annectens*, it is mentioned that the specimens from Berkeley, Walnut Creek, and Mount Diablo, though identified as *annectens*, are similar in cranial

characters to *riparia*, and grade toward this race in pelage characters. At the present time, no area suitable for wood-rat inhabitation is known to exist, even by way of the oak-studded San Joaquin River bottom lands, between the type locality of *riparia* and the East Bay region. However, before the extensive cultivation of the San Joaquin Valley by the white man, and the denudation of the foothills by his domestic animals (resulting in a lowering of the water table and a consequent drying of stream beds and removal of riparian vegetation), the type of habitat required for wood rat subsistence may have been present continuously in some territory connecting the East Bay region with the region of the type locality of *riparia*.

*Specimens examined*.—A total of 7 from the following localities in California: *San Joaquin County*: San Joaquin River, 3 mi. NE Vernalis, 5. *Stanislaus County*: Kincaid's Ranch, 2 mi. NE Vernalis, 2.

*Neotoma fuscipes perplexa*, new subspecies  
Diablo Range Wood Rat

*Neotoma fuscipes annectens*, Goldman (1910:90-91), part.

*Type*.—Adult female, skin and skull; no. 14079, Mus. Vert. Zööl.; Sweeney's Ranch, 22 miles south of Los Banos, Merced County, California; collected March 30, 1911, by W. L. Chandler and C. H. Richardson; original no. 65, C. H. R.

*Range*.—In general, Diablo Range, and region south of Monterey Bay east of Salinas Valley. More specifically, from region of Suisun Straits, southward along slopes of Diablo Range to northern San Benito County, thence west to Salinas River and south to extreme southern Monterey County and vicinity of Coalinga, Fresno County. Vertical range from 500 feet at 5 miles east of Coalinga, Fresno County, to 2400 feet in Priest Valley, Monterey County. Zonal range Lower Sonoran and Upper Sonoran.

*Diagnosis*.—Size: medium (see under "Measurements"). Color: moderately pale, resembling *N. f. riparia*, but purer cinnamon dorsally. Skull: similar to *annectens*, but rostrum relatively broader and shorter; distinct from other forms of group B in its shorter, broader incisive foramina; bullae moderately large; zygomata moderately expanded.

*Color*.—Cinnamon to Vinaceous Cinnamon dorsally, with fewer black and black-tipped hairs than in *monochrourea* (mass effect thus much lighter and of purer cinnamon color), lighter on sides, white beneath (with belly hairs, to a greater or less degree, plumbeous at base and lightly overlaid with cinnamon); forefeet usually white from immediately below the ankles posteriorly to toes (sometimes lightly clouded with dusky); toes white; tail dark above, lighter below.

*Skull*.—In essential features resembling *annectens* but with the following differences: size smaller; rostrum proportionately broader and shorter; incisive foramina averaging shorter, and more expanded laterally; diastema less arched (nearer a horizontal plane, when viewed laterally); total length of incisive foramen and palatal bridge less.

*Comparisons*.—*N. f. perplexa* can be distinguished readily from *bullator* by its smaller size; darker, more reddish coloration; smaller ears; shorter incisive foramina; and less inflated bullae. For comparisons with other subspecies, see preceding descriptions and account of *riparia*.

*Remarks*.—The race *perplexa* occupies much of the warmer, more arid slopes of the inner Coast Range in west-central California. It intergrades with the darker coast forms to the west, and with the more pallid San Joaquin Valley and Temblor Range forms to the north and south, respectively. Specimens from 5 miles east of Coalinga, Fresno County, approach *bullator* in their larger size, larger ears, and paler color, but lack the highly inflated

bullae characteristic of that race. Specimens from Jolon, Monterey County, here referred to *luciana*, approach *perplexa* in color, shape of interpterygoid fossa, and size of auditory bullae; however, in all other characters, they are more similar to *luciana*. For further discussion of intergradation, see accounts of *luciana* and *annectens*.

*Specimens examined*.—A total of 97 from the following localities in California: *Fresno County*: Arroyo Pasajero, 5 mi. E Coalinga, 1 (Coll. W. T. Shaw); Pleasant Valley Stock Farm, 5 mi. E Coalinga, 600 ft., 4 (Coll. J. R. Arnold, 1; Mus. Vert. Zool., 3). *Merced County*: Sweeney's Ranch, 22 mi. S Los Banos, 5. *Monterey County*: Lewis Creek, 1750 ft., 1 (Coll. O. P. Silliman); Priest Valley, 2400–2500 ft., 11 (Coll. O. P. Silliman, 1; U. S. Nat. Mus., Biol. Surv. Coll., 10); 1½ mi. S Soledad, 182 ft., 4; Stonewall Creek, 1300 ft., 6¾ mi. NE Soledad, 13 (Coll. O. P. Silliman, 5; Mus. Vert. Zool., 8). *San Benito County*: near Cook Post Office, 1300 ft., Bear Valley, 13; 3½ mi. W Hernandez, 3000 ft., 1; 4 mi. S Hernandez, 4000 ft., Laguna Ranch, 5; 2 mi. NNE New Idria, 1900 ft., 3; Panoche Creek, 1700 ft., above Cherry Hill, 1 (Coll. Fresno State College); Panoche Creek, 1200 ft., 2 mi. SE Panoche, 12; 6 mi. ESE San Benito, 1600 ft., 7; 5 mi. NNE San Benito, 3000 ft., Butts Ranch, 7; 1 mi. SE summit San Benito Mountains, 4400 ft., 8.

***Neotoma fuscipes bullator*, new subspecies**  
**San Miguel Wood Rat**

*Neotoma fuscipes annectens*, Goldman (1910:90–91), part.

*Type*.—Adult female, skin and skull; no. 28900, Mus. Vert. Zool.; 2 miles south of San Miguel, 620 feet altitude, San Luis Obispo County, California; collected November 9, 1918, by R. Hunt; original no. 742.

*Range*.—From immediate vicinity of type locality southeastward through Temblor Range and southern end of Diablo Range to southern end of hills (east of Pine Mountains) bounding Carrizo Plains, in extreme southeastern San Luis Obispo County; in brief, chiefly area drained by Cholame, Estrelia, and San Juan creeks. Known vertical range 620 feet to 2600 feet. Zonal range Lower Sonoran and Upper Sonoran.

*Diagnosis*.—Size: large; ears and hind feet large (see under "Measurements"). Color: pale, resembling *N. f. simplex* from San Emigdio Creek, Kern County, but more grayish buff dorsally. Skull: similar to that of *riparia*, but with zygomata less spreading, evenly rounded (rather than angular), and more depressed ventrally; auditory bullae most highly inflated of any subspecies of *fuscipes* group; rostrum long, broad, and tapering comparatively little anteriorly.

*Color*.—Pinkish Buff to Pinkish Cinnamon, dorsally; feet white above; tail distinctly bicolored; similar to *N. f. fuscipes*, but with hairs of belly plumbeous at base; similar to *N. f. simplex*, but more buffy dorsally; throat, chest, and inguinal regions pure white throughout.

*Skull*.—Similar to *riparia*, but bullae more highly inflated and zygomata less angular, more narrow, and noticeably depressed ventrally.

*Comparisons*.—The race *bullator* can be distinguished from the race *annectens* by the following characters: size larger, with larger ears, longer tail and hind feet; color darker, with bicolored tail and white hind feet; skull deeper and less angular; rostrum heavier; bullae more highly inflated; anterosuperior border of meatus projecting less strongly. From *perplexa*, it differs conspicuously in larger size; lighter, more buffy color; more depressed zygomata; and larger bullae.

*Remarks*.—Two specimens in juvenile pelage from Carrizo Plains and Santiago Springs both exhibit the cranial characters of group B, and, on the basis of large ears, large auditory bullae, and heavy rostrum, are referred to the race *bullator*. No intergradation with *simplex* is known. For evidences of intergradation with *perplexa* and *luciana*, see accounts of those forms.



*Specimens examined*.—A total of 9 from the following localities in San Luis Obispo County, California: Carrizo Plains, 1 (U. S. Nat. Mus., Biol. Surv. Coll.); San Diego Joe's [U. S. G. S. sheet, edition of 1913], 16 mi. SW McKittrick [specimen label reads: Santiago Springs, 16 mi. SW McKittrick, Kern County], 1 (U. S. Nat. Mus., Biol. Surv. Coll.); 2 mi. S San Miguel, 7.

***Neotoma fuscipes streatori* Merriam**

Streator Wood Rat

*Neotoma fuscipes streatori* Merriam (1894a:124).

*Neotoma fuscipes*, Price (1893:329), part.

*Type*.—Adult male; no. 64439, U. S. Nat. Mus., Dept. Agr. Coll.; Carbondale, Amador County, California; collected April 4, 1894, by Clark P. Streator; original no. 3685 (Merriam, *loc. cit.*).

*Range*.—Western slope Sierra Nevada Range, from southeastern Tehama County south to central Tulare County; entirely west of Sierran crest; east at south of San Joaquin Valley floor and at north of Sacramento River. Vertical range from 200 feet on Butte Creek, Butte County, and at Minkler, Fresno County, to 5000 feet in Kings River Canyon, Fresno County. Zonal range Upper Sonoran into Transition.

*Diagnosis*.—Size: small (see under "Measurements"). Color: similar to *N. f. fuscipes*, but more grayish and buffy dorsally, with more extensive plumbeous area on belly, and tail darker above. Skull: small, evenly arched and deep; palatal bridge short (less than 8.4 mm. in specimens examined, shorter than molar row and appearing shorter than incisive foramen); interpterygoid fossa moderately wide, but rarely spatulate.

*Color*.—Nearest Cinnamon-Buff dorsally, but mass effect appearing grayer because of presence of numerous black and black-tipped hairs; hairs of chest, inguinal region, and dorsal sides of hind feet pure white throughout; hairs of belly most often plumbeous at base and tipped with light Cinnamon-Buff or white; hairs of throat most often white throughout, but in a few specimens lightly plumbeous at base and Cinnamon-Buff at tips; tail dark brown above, white below. Similar to *fuscipes*, but more grayish and buffy above (color nearest Pinkish Cinnamon in *fuscipes*), and area on belly with hairs lead colored to base more extensive; hind feet white above (dusky plus or minus 1 cm. below ankles in *fuscipes*). Much darker and more grayish than *simplex*.

*Skull*.—Intermediate in character between groups A and C; similar to *macrotis* of group C, but differing in the following respects: skull deeper; zygomata more spreading; nasals shorter; rostrum averaging broader; palatal bridge averaging shorter; interpterygoid fossa narrower and less spatulate. Differs from *monochoura* of group A as follows: size smaller (well seen in shorter nasals; shorter, narrower, and shallower rostrum; shorter palatal bridge; and smaller and less inflated bullae); incisive foramina shorter and more concave laterally; interpterygoid fossa more rounded, approaching the spatula shape found in group C.

*Comparisons*.—The race *streatori* resembles most closely the race *simplex* of group C and the race *fuscipes* of group A; it requires further comparison with these two forms only. From *simplex*, it can be readily distinguished by the slightly smaller size, darker, more grayish coloration, shorter nasals, smaller bullae, proportionately less breadth to depth of rostrum, and less spatulate interpterygoid fossa. From *fuscipes*, it differs in smaller size, more grayish and buffy color above and more extensive area of lead-colored hairs below, shorter rostrum, shorter palatal bridge, smaller bullae, and wider, more rounded interpterygoid fossa.

*Remarks*.—Except in the areas of intergradation, throughout its range *N. f. streatori* exhibits comparatively few variations in the characters studied. Specimens from the Yosemite region vary somewhat in ventral coloration, ranging from pure white throughout to a cinnamon color deeper than that exhibited by a series of topotypes; however, in dorsal coloration and in cranial characters, they are closely similar to specimens from the type locality or from

other localities throughout the range of the race. Through Butte and Tehama counties the race intergrades with *fuscipes*. Specimens from near Oroville and Chico, Butte County, exhibit the large size, cinnamon coloration dorsally, white belly (with smaller plumbeous area), dusky feet, and narrow interpterygoid fossa characteristic of the race *fuscipes*. However, in less angular zygomata, shorter rostrum, smaller and less inflated bullae, they are similar to typical *streator*, and are herewith referred to this race. Specimens examined from localities in Tehama County including and north of the town of Tehama are extremely variable in skin and skull characters, and, although all are intermediate in these characters between *fuscipes* and *streator*, have been referred to the Sacramento Valley race, *fuscipes*. All specimens examined from localities in Tulare County are intermediate between *streator* and *simplex* in the characters studied. Intergradation of these two races is thus indicated. Two specimens from 4 miles east of Porterville and from 8 miles east of White River are, to me, nearer *simplex* in coloration, in size of bullae, and in the diagnostic characters of the rostrum. Four animals from 7 miles west of Orosi, though resembling closely the afore-mentioned specimens in coloration, exhibit the smaller size, smaller bullae, and characters of the rostrum which have been ascribed to *streator*.

*Specimens examined*.—A total of 129 from the following localities in California: *Amador County*: Carbondale, 10 (U. S. Nat. Mus., Biol. Surv. Coll.); 5 mi. E Carbondale, 500 ft., 7. *Butte County*: Chambers Ravine, 600 ft., 4 mi. N Oroville, 13; Butte Creek, 200 ft., 4 mi. SE Chico, 8. *Eldorado County*: 1 mi. NW Fyffe, 3500 ft., 3; Limekiln, Middle Fork American River, 1200 ft., 2. *Fresno County*: 3 mi. SE Friant, 2; Kings River Canyon, 5000 ft., 1; Minkler, 200 ft., 1. *Madera County*: Raymond, 940 ft., 3. *Mariposa County*: Cascades, Yosemite Park, 2; 3 mi. NE Coulterville, 3200 ft., 2; 1 mi. W Coulterville, 1600 ft., 1; El Portal, 11; 1¼ mi. W El Portal, 1800 ft., 3; Dudley, 3000 ft., 1; 7 mi. E Mariposa, 1; Pleasant Valley, 600–700 ft., 9; Sweetwater Creek, 3800–3950 ft., 2 mi. E Feliciana Mountain, 4; Yosemite Valley, 4000 ft., 3. *Placer County*: Blue Canyon, 4600 ft., 1; Dutch Flat, 3400 ft., 5; Michigan Bluff, 3500 ft., 1. *Tehama County*: Dale's, Payne Creek, 600 ft., 3; Lyman's, 3300 ft., 4 mi. NW Lyonsville, 5; Manton, 2300 ft., 9; Mill Creek, 2 mi. NE Tehama, 260 ft., 12; Payne Creek Post Office, 1600 ft., 1; 1 mi. NE Red Bluff, 300 ft., 1. *Tulare County*: Canyon Creek, 700 ft., 7 mi. W Orosi, 4 (Coll. W. B. Richardson).

#### *Neotoma fuscipes simplex* True

##### Fort Tejon Wood Rat

*Neotoma macrotis simplex* True (1894:354).

*Neotoma fuscipes dispar* Merriam (1894a:124–125). Type from Lone Pine, Inyo County, California.

*Neotoma fuscipes simplex*, Miller and Behn (1901:105).

*Neotoma fuscipes mohavensis* Elliot (1903:246–247). Type from Oro Grande, San Bernardino County, California.

*Neotoma fuscipes cnemophila* Elliot (1904:267–268). Type from Mount Pinos, Ventura County, California.

*Type*.—Adult male, skin and skull; no.  $\frac{3651}{3597}$  U. S. Nat. Mus.; Fort Tejon [Kern County], California; collected by J. Xantus [sometime between July, 1857, when Xantus first arrived at Fort Tejon (Harris, 1934:199), and March 24, 1859, the date the type specimen was entered in the catalogues of the U. S. Nat. Mus.]; original no.  $\frac{785}{786}$  (see Lyon and Osgood, 1909:104–105).

*Range*.—Eastern and southeastern basal slopes of southern Sierra Nevada, Inyo, and Kern counties, south through Tehachapi region, Kern County, thence southeastward along northern slopes of San Gabriel Mountains, Los Angeles and San Bernardino counties, through the San Bernardino Mountains in extreme southern San Bernardino County. Vertical range from approximately 400 feet on the north side of Buena Vista Lake, Kern County, to 9000 feet at Dry Lake, San Bernardino Mountains, San Bernardino County. Zonal range chiefly Upper Sonoran, but extending from Lower Sonoran into Transition.

*Diagnosis*.—Size: medium (see under "Measurements"). Color: pale; Pinkish or Vinaceous Cinnamon dorsally, resembling *N. f. fuscipes* from Glenn and Colusa counties, but with more ventral pigmentation. Skull: similar to *luciana*, but more flattened dorso-ventrally and with shorter molar series; rostrum broad and relatively short; diastema relatively straight in outline (when viewed laterally), but meeting molar parts of maxillae at an abrupt angle, making molar rows more elevated from horizontal plane of diastema than in other forms of group C.

*Color*.—Essentially that of *N. f. fuscipes*, but appearing paler dorsally, and with hairs of belly plumbeous at base (and often overlaid with Pinkish or Vinaceous Cinnamon).

*Skull*.—Similar to *luciana*, but with differences as follows: averaging deeper, narrower, and less flattened in dorsal outline (when viewed laterally); rostrum averaging longer and shallower; molar row averaging shorter.

*Comparisons*.—On the basis of external characters, *simplex* is distinguishable from *luciana* and *macrotis* by its larger size, paler dorsal coloration, and white hind feet. In cranial characters, it differs from *macrotis* as follows: deeper and less angular skull; larger size; shorter and broader rostrum; more wide-spreading and angular zygomata; larger and more discoidal-shaped bullae; diastema relatively straight in outline (as in *macrotis*), but meeting molar parts of maxillae at a more acute angle, making molar rows more elevated from horizontal plane of diastema. For further comparison with *luciana* and with *streatori* see accounts of those forms.

*Remarks*.—The several subspecific names that have been proposed for animals here referred to *simplex* indicate, to some degree, the extreme variability of this race. *N. f. simplex* ranges from the warm, dry Lower Sonoran zone of the Mohave Desert and San Joaquin Valley, up through the foothills and valleys of the more ecologically diverse Upper Sonoran zone, into the cooler, coniferal belt of the Transition zone, on higher mountains, and is subjected to a topographical and climatic diversity perhaps more extreme than that met by any other subspecies of the *fuscipes* series. Though many local variations do occur, none of them seems to me to be of sufficient constancy and magnitude to warrant subspecific recognition. Specimens from Oro Grande, San Bernardino County, which form the basis for the name *mohavensis*, do not differ markedly, in any of the characters studied, from typical specimens of *simplex*. Nine specimens at hand from Mount Pinos, the type locality of *N. f. cnemophila*, vary noticeably in color, and grade toward *macrotis*. Specimens from near Lone Pine, Inyo County, the type locality of *dispar*, and Walker Pass, Kern County, have very few black and black-tipped hairs and are thus extremely pale in color. However, this extreme is within the range of variation of *simplex*. For additional information concerning intergradation with adjoining subspecies, see accounts of *streatori*, *macrotis*, and *bullator*.

*Specimens examined*.—A total of 203 from the following localities in California: Inyo County: Carl Walter's Ranch, 2 mi. N Independence, 1; Carroll Creek, 5500 ft., 2; Lone Pine Creek, 4500 ft., 25; Kearsarge Pass, 6000 ft., Sierra Nevada, 2. Kern County: Buena

Vista Lake, N side, 4 (U. S. Nat. Mus., Biol. Surv. Coll.); head of Cuddy Valley, 5900 ft., 2; Fay Creek, 4100 ft., 6 mi. N Weldon, 3; Fort Tejon, 3; French Gulch, 6700 ft., Piute Mountains, 5; Keavah Mountain, 7000 ft., Walker Pass, 2; NW part Kelso Valley, 4100 ft., 1; Kern River at Bodfish, 2400 ft., 2; Mount Pinos, 5000–6000 ft., 10 mi. W Lebec, 4 (Coll. J. C. von Bloeker, Jr.); Onyx, 2750 ft., 2; Piute Mountains, 1; Rankin Ranch, 3300 ft., Walker Basin, 5; Rip Rap Mine, Piute Mountains, 2; San Emigdio Creek, 1500 ft., 17; 2 mi. N Sorrell Ranch, 4500 ft., Kelso Valley, 1; 1½ mi. N Tehachapi, 4250 ft., 2; Thompson Canyon, 3900 ft., Walker Basin, 13; Walker Basin, 3300 ft., 1; W slope Walker Pass, 4600 ft., 5; Weldon, 2650 ft., 3. *Los Angeles County*: Fairmont, 1 (Coll. J. C. von Bloeker, Jr.); 3 mi. W Fairmont, 2900 ft., 1; Gorman, 2; Llano, 2500 ft., 1 (Coll. J. C. von Bloeker, Jr.). *San Bernardino County*: Oro Grande, 2700 ft., 1; ½-mi. N Oro Grande, 2700 ft., 2; Victorville, Mohave River, 5. The following localities in San Bernardino Mountains: Cactus Flat, 6000 ft., 2; Dobie, 7000 ft., 5; Dry Lake, 9000 ft., 1; Fish Creek, 6500 ft., 27; Forsee Creek, 4500 ft., 3; Santa Ana Canyon, 3000 ft., 2; Santa Ana River, 5500 ft., 1; South Fork Santa Ana River, 6200 ft., 2; Saragossa Springs, 7530 ft., 1; Seven Oaks, 5000–5100 ft., 14; Sugarloaf, 7500 ft., 14. *Tulare County*: Posey Creek, 2200 ft., 8 mi. E White River, 1 (Coll. W. B. Richardson); Rocky Hill, 4 mi. E Porterville, 1 (Coll. W. B. Richardson); Taylor Meadow, 7000 ft., Sierra Nevada, 2. *Ventura County*: Cuddy Canyon, 4400 ft., Frazier Mountain, 1; Mount Pinos, 5500–6500 ft., 5.

*Neotoma fuscipes luciana*, new subspecies

Santa Lucia Wood Rat

*Neotoma fuscipes macrotis*, Goldman (1910:93–94), part.

*Type*.—Adult female, skin and skull; no. 29321, Mus. Vert. Zool.; Seaside, Monterey County, California; collected December 17, 1918, by H. G. White; original no. 2884.

*Range*.—Coastal central California, from Monterey Bay southward through Santa Lucia Mountains to vicinity of Paso Robles and Morro, San Luis Obispo County. Vertical range from near sea level at least to 3000 feet at 1¼ miles south of Chalk Peak, Monterey County. Zonal range Upper Sonoran into Transition.

*Diagnosis*.—Size: medium (see under "Measurements"). Color: dark, similar to *macrotis*. Skull: similar to *simplex*, but deeper dorsoventrally; brain case short as in *macrotis*, but broader; spread of zygomata moderate; bullae small; rostrum proportionately most short and broad of any subspecies of *N. fuscipes*.

*Color*.—Intermediate in characteristic features between *monochroua* and *macrotis*, with tail coloration as in *macrotis*.

*Skull*.—In essential features similar to *macrotis*, but conspicuously larger, with broader brain case, wider spreading zygomata, and much longer and heavier molar row.

*Comparisons*.—For comparison with *macrotis*, see descriptions above. From *streatori*, *luciana* can be distinguished by the following characters: color darker and less grayish; hind feet clouded with dusky (instead of white throughout); brain case broader; rostrum broader and shorter; nasals longer; interpterygoid fossa averaging broader; bullae slightly larger. It differs from *simplex* in its darker coloration, dusky hind feet, deeper skull (less flattened dorsoventrally), heavier rostrum, and longer molar row.

*Remarks*.—*N. f. luciana* does not differ markedly from *macrotis* or *anneotens* in external characters, but is distinguishable from both by well-marked cranial characters. Where its range meets that of each adjoining subspecies, intergradation occurs. Specimens from Camp Ord, 3½ miles east of Marina, Monterey County, resemble *anneotens* from San Mateo County in all but two diagnostic characters of skin and skull. In these specimens the shape of the interpterygoid fossa is broad and spatulate and the outline, posteriorly, of the palatal bridge is slightly concave. In these features these specimens are similar to *luciana*. One specimen of 5 from Indian Harbor, 1½ miles south of Marina, Monterey County, has the interpterygoid fossa narrower than it is in

the other specimens from this locality; in this respect it approaches *annectens*. Other diagnostic characters both of this specimen and of the others from this locality are more like those seen in *annectens*.

Specimens from the Salinas Valley at San Ardo and 5 miles south of San Ardo, Monterey County, indicate gradation of *luciana* toward *perplexa*. In larger general body size, larger ears, lighter coloration, moderately inflated bullae, and greater total length of palatal bridge and incisive foramen they resemble *perplexa*. However, the comparatively shorter palatal bridge, less massive molars, shorter molar row, wider interpterygoid fossa, and concave posterior border of the palatal bridge are typical of the race *luciana*; here they are included with this subspecies.

*Specimens examined*.—A total of 108 from the following localities in California: *Monterey County*: Abbott's Ranch, Arroyo Seco, 2; Big Sur River, 4; Camp Ord, 3½ mi. E Marina, 100 ft., 4 (Coll. O. P. Silliman); 1¼ mi. S Chalk Peak, 3000 ft., 4; Chew's Ridge, 5000 ft., Santa Lucia Mountains, 7 (Coll. O. P. Silliman); China Camp, 4500 ft., Santa Lucia Mountains, 3 (Coll. O. P. Silliman); Garrapatos Creek, 49 ft., Santa Lucia Mountains, 1 (Coll. O. P. Silliman); Indian Harbor, 1½ mi. S Marina, 50 ft., 5 (Coll. O. P. Silliman); Jolon, 4; Limekiln Creek, 250 ft., Santa Lucia Mountains, 7 (Coll. O. P. Silliman); Monterey, 14 (Coll. O. P. Silliman, 1; Mus. Vert. Zool., 13); 2 mi. S Monterey, 1; Salinas Valley, 450 ft., San Ardo, 4 (Coll. O. P. Silliman); 5 mi. S San Ardo, 1 (Coll. O. P. Silliman); San Lucas, 3; 2 mi. E San Lucas, 397 ft., 4; ¾-mi. S San Lucas, 397 ft., 2; Seaside, 9; 1 mi. NE Seaside, 1; Upper San Antonio Creek, 1; Wildcat Canyon, 1. *San Luis Obispo County*: Cambria, 5; De Tracey Ranch, 1250 ft., Santa Lucia Mountains, 5 (Coll. O. P. Silliman); 1 mi. NE Morro, 2; 4½ mi. S Morro, 2; Paso Robles, 750 ft., 5 (U. S. Nat. Mus., Biol. Surv. Coll.); San Carpojo Creek, 7 mi. N Piedras Blancas, 8.

#### *Neotoma fuscipes macrotis* Thomas

San Diego Wood Rat

*Neotoma macrotis* Thomas (1893:234-235).

*Neotoma fuscipes macrotis*, Merriam (1894b:246).

*Type*.—Adult male [in alcohol]; no. 93.2.2.4, British Museum; San Diego, San Diego County, California; collected by Professor [Carl H.] Eigenmann (see Goldman, 1910:93) sometime in period 1889-1891, when Eigenmann worked in San Diego (Eigenmann, 1892).

*Range*.—In general, coastal southern California and northern Lower California; from Santa Margarita (west of Pine Mountains), San Luis Obispo County, southward through mountains of Ventura and Santa Barbara counties, along southern drainage of San Gabriel Mountains, through San Jacinto and Palomar mountains to the vicinity of Los Pozos, Lower California (at latitude 32 degrees north, approximately). Vertical range from near sea level to 6800 feet on Thomas Mountain, Riverside County. Zonal range from Lower Sonoran into Transition.

*Diagnosis*.—Size: small (see under "Measurements"). Color: dark; Pinkish Buff above; hind feet dusky. Skull: narrow, shallow, and lacking marked angularity; rostrum narrow and relatively long, similar to *martirensis*, but deeper; zygomata spreading narrowly and evenly, lacking angularity; palatal bridge conspicuously shorter than incisive foramina or molar row; interpterygoid fossa broad and spatulate; auditory bullae small, and globular in shape, distinctly removed from foramen ovale in comparison with *luciana* from coastal Monterey County.

*Color*.—Pinkish Buff dorsally, appearing grayer because of presence of more black and black-tipped hairs (but less grayish than in *streatori*); underparts white, the fur plumbeous at base across belly and often overlaid with Pinkish Buff; tail dark above, lighter below; forefeet dusky, or white throughout; hind feet clouded with dusky to toes; toes white. Similar to *monochrourea*, but dorsal coloration more buffy (less cinnamon-colored) and tail not unicolored.

*Skull*.—Small, narrow, shallow, and lacking marked angularity; rostrum relatively long, and narrowest of all races of *fuscipes*; nasals long and flared anteriorly; zygomata narrowly spreading, and merging gradually posteriorly with skull, rather than at an abrupt angle as in *annectens*; palatal bridge short (apparently much shorter than incisive foramen and approximately 1 mm. shorter than length of upper-molar series) and usually concave in outline posteriorly; incisive foramina long and narrow, usually extending posteriorly to anterior plane of first molars; interpterygoid fossa wide and spatulate; auditory bullae small and globular in shape, with anteromost border of inflated part usually 1 mm. or more from foramen ovale; anterosuperior border of meatus projecting weakly.

*Comparisons*.—The race *macrotis* requires comparison only with members of group C. From *streatori*, it differs in the following characters: color darker, with more cinnamon pigmentation dorsally and ventrally; hind feet dusky above; skull narrower; zygomata less widely spread; rostrum conspicuously narrower; incisive foramina less expanded laterally; interpterygoid fossa broader and more spoon shaped. For comparisons with *simplex*, *luciana*, and *martirensis*, see accounts of those forms.

*Remarks*.—The range of *N. f. macrotis*, as hereby defined, allows for intergradation of the race with four subspecies, namely, *luciana*, *bullatior*, *simplex*, and *martirensis*. Specimens from Santa Margarita, San Luis Obispo County, though definitely referable to *macrotis*, grade toward *luciana* in all characters studied. From extreme southeastern Kern County and northern Ventura County, southeast along the Sierra Madre, San Gabriel, San Bernardino, and San Jacinto mountains, specimens are intermediate in character between *macrotis* and *simplex*, indicating intergradation with the latter race. In the San Bernardino, San Jacinto, and Palomar mountains, the great variation which occurs makes identification difficult. However, none of these variations seems to me to be sufficiently constant to warrant subspecific designation. Therefore, I have relegated the name *mohavensis* of Elliot (1903:246–247) to synonymy under *simplex*, since specimens from Oro Grande, the type locality of *mohavensis*, are referable to *N. f. simplex*. The pale, dorsal coloration characteristic of *simplex* persists along the eastern border of the range of *simplex* as far south as the Palomar Mountains, San Diego County. However, in most of the specimens from this area, including those having the dorsal coloration of *simplex*, the hind feet are usually clouded with dusky above, as in *macrotis* from coastal San Diego County. In cranial characters, specimens from the San Bernardino Mountains are similar to topotypes of *macrotis* in smaller size (well seen in narrow spread of zygomata), are intermediate between *macrotis* and *simplex* in outline of diastema, but are similar to *simplex* in the following diagnostic characters of the rostrum: greater breadth, greater depth, and breadth approximately equal to depth. Specimens from the San Jacinto and Palomar mountains, though grading toward *simplex* in skull characters, are nearer *macrotis*. Therefore, on the basis of total number of characters, the line of demarcation separating the races *simplex* and *macrotis* has been placed between the San Bernardino and the San Jacinto mountains. On the average, specimens from localities to the north of this line show greater similarity to *simplex*, whereas those from localities to the south are nearer *macrotis*. All may be termed “intergrades.” For description of intergradation with *martirensis*, see account of that race.

*Specimens examined*.—A total of 203 from the following localities: **California:** *Los Angeles County:* Arroyo Seco, near Pasadena, 9; Eaton Wash, 3; Glendora, 1; Linda Vista, 4; Oak Knoll, near Pasadena, 1; Tijuana Valley, 5. *Orange County:* Trabuco Canyon, 1500–1700 ft., 12. *Riverside County:* near Cabazon, 1700 ft., base of San Jacinto Mountains, 4; Garnet Queen Mine, 6000 ft., Santa Rosa Mountains, 11; Kenworthy, 4500 ft., San Jacinto Mountains, 9; Schain's Ranch, 4900 ft., San Jacinto Mountains, 20; Strawberry Valley, 6000 ft., San Jacinto Mountains, 5; Thomas Mountain, 6800 ft., 5. *San Bernardino County:* Bear Flat, 6500 ft., San Antonio Canyon, San Gabriel Mountains, 2; 2 mi. NE Grapeland, 2000 ft., 1. *San Diego County:* Campo, 2; Cuyamaca Mountains, 12; Dulzura, 3; Escondido, 3; 6 mi. N Foster, 2; junction of Gopher Canyon and San Luis Rey River, 1; Julian, 4; Pine Mountains, 2750 ft., 1; San Diego, 26; near mouth of Tia Juana River, 4; Warner Pass, 11; Witch Creek, 3. *San Luis Obispo County:* Santa Margarita, 996 ft., 25. *Ventura County:* Matilija, 5; 7 mi. S Simi, 1; Ventura, 3. **Lower California:** Los Pozos, 4200 ft., Sierra Juarez, 2; 5 mi. S Monument 258, west coast Lower California, 1; north end Nachoguero Valley, 3400 ft., 2.

***Neotoma fuscipes martirensis* Orr**  
San Pedro Mártir Wood Rat

*Neotoma fuscipes martirensis* Orr (1934:110–111).

*Neotoma fuscipes*, Allen (1893:185), part.

*Neotoma macrotis* Thomas (1893:234–235), part.

*Neotoma fuscipes macrotis*, Merriam (1894b:246), part.

*Type*.—Adult male, skin and skull; no. 35850, Mus. Vert. Zool.; Valladares, 2700 feet altitude, Sierra San Pedro Mártir, Lower California, Mexico; collected April 15, 1925, by A. E. Borell and C. C. Lamb; original no. 1419, A. E. B.

*Range*.—Chiefly Sierra San Pedro Mártir region of Lower California, but occurring intermittently to coast, northward to approximately 32 degrees north latitude and southward at least to 30 degrees north latitude. Known vertical range from 25 feet to 8500 feet. Zonal range Lower Sonoran into Transition.

*Diagnosis*.—Size: small (see under "Measurements"). Color: dark; similar to *N. f. macrotis*, but with greater amount of ventral pigmentation, on the average. Skull: small; not markedly arched when viewed laterally, and lacking marked angularity (even in old specimens); zygomata little spreading; rostrum shallow (6.5 mm.–7.3 mm. in specimens examined); molar row short; total length of palatal bridge and incisive foramen small (maximum 18 mm. in females examined); bullae small.

*Color*.—Essentially that of *macrotis*, but with more pigmentation ventrally.

*Skull*.—Resembling that of *N. f. macrotis*, but averaging smaller in size (well seen in shorter nasals), and rostrum conspicuously shallower.

*Comparisons*.—*N. f. martirensis* can be readily distinguished from all other races of the species by its smaller size and shallow rostrum, in combination with the characters which serve to distinguish *macrotis* from the more northern subspecies of *N. fuscipes*.

*Remarks*.—Intergradation with *macrotis* occurs between latitude 32 degrees north and the International Boundary. An adult specimen from Las Cruces, 20 miles east of Ensenada, and one adult and two juveniles from Laguna Hansen, Lower California, exhibit the characters attributed to *martirensis*. Two juveniles at hand from Los Pozos are too young to permit definite subspecific identification, but because of their comparatively deep rostra they are referred to *macrotis*. The intensity and extent of cinnamon, ventral pigmentation varies to such a degree in both *macrotis* and *martirensis* that specimens exhibiting this feature can be identified with certainty only by reference to the skulls.

*Specimens examined.*—A total of 30 from the following localities in **Lower California**: Aguaje del Sauce, 2600 ft., 6 mi. NW Valladares, 2; Concepción, 6000 ft., Sierra San Pedro Mártir, 1; 1 mi. E El Rosario, 200 ft., 4; La Grulla, 7200–7500 ft., Sierra San Pedro Mártir, 8; Laguna Hansen, 5200 ft., Sierra Juarez, 3; Las Cruces, 2600 ft., 20 mi. E Ensenada, 2; San José, latitude 31 degrees N, 2300–2500 ft., 5; Santa Domingo, 25 ft., 1; Valladares, 2700 ft., 3; Vallecitos, 8500 ft., Sierra San Pedro Mártir, 1.



TABLE 1  
AVERAGE AND EXTREME MEASUREMENTS IN MILLIMETERS OF ADULT FEMALES OF ELEVEN SUBSPECIES OF *Neotoma fuscipes*  
(Key numbers indicate number of specimens examined if fewer than that indicated by subspecies headings)

| Total length                                                               | Tail vertebrae              | Hind foot                | Ear, from anterior notch | Basilar length                 | Zygomatic breadth              | Length of nasals               | Depth of skull                 | Breadth of rostrum | Depth of rostrum | Inter-orbital breadth | Length of incisive foramen | Length of palatal bridge | Sum of foramen and bridge | Length of upper-molar series | Breadth of bulla |
|----------------------------------------------------------------------------|-----------------------------|--------------------------|--------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------|------------------|-----------------------|----------------------------|--------------------------|---------------------------|------------------------------|------------------|
| <i>N. f. monochrourea</i> , 7 ♀, 7 mi. W Cazadero                          |                             |                          |                          |                                |                                |                                |                                |                    |                  |                       |                            |                          |                           |                              |                  |
| 419 <sup>a</sup><br>403-463                                                | 207 <sup>a</sup><br>192-241 | 40<br>38-44              | 25<br>24-27              | 39.4 <sup>a</sup><br>38.7-40.8 | 25.3 <sup>a</sup><br>24.3-26.1 | 18.2<br>17.4-19.1              | 16.3 <sup>a</sup><br>15.5-16.8 | 7.4<br>6.8-7.7     | 7.5<br>7.1-7.9   | 5.9<br>5.4-6.3        | 10.4<br>9.8-11.3           | 8.9<br>8.3-9.5           | 19.3<br>18.5-20.8         | 9.4<br>9.2-9.5               | 7.5<br>7.1-8.2   |
| <i>N. f. fuscipes</i> , 4 ♀, Colusa and Glenn counties                     |                             |                          |                          |                                |                                |                                |                                |                    |                  |                       |                            |                          |                           |                              |                  |
| 405<br>384-428                                                             | 192<br>182-211              | 40<br>37-43              | 27<br>26-29              | 40.0 <sup>a</sup><br>38.4-41.1 | 25.0<br>23.7-25.7              | 19.0<br>18.0-20.1              | 16.1 <sup>a</sup><br>15.5-17.0 | 7.3<br>6.9-7.8     | 7.5<br>7.2-7.8   | 6.0<br>5.6-6.6        | 10.8<br>10.4-11.1          | 8.6<br>8.3-8.8           | 19.4<br>18.7-19.9         | 9.5<br>9.2-9.7               | 8.0<br>7.9-8.2   |
| <i>N. f. annexens</i> , 10 ♀, San Mateo and (western) Santa Clara counties |                             |                          |                          |                                |                                |                                |                                |                    |                  |                       |                            |                          |                           |                              |                  |
| 428 <sup>7</sup><br>418-444                                                | 212 <sup>7</sup><br>193-227 | 41 <sup>a</sup><br>40-42 | 28<br>26-29              | 40.5<br>38.7-42.7              | 25.8<br>24.9-26.4              | 18.8<br>18.0-19.9              | 16.7<br>16.0-17.2              | 7.5<br>7.0-7.8     | 7.8<br>7.3-8.1   | 5.7<br>5.4-6.2        | 10.7<br>10.0-11.1          | 9.1<br>8.6-10.0          | 19.8<br>19.2-20.9         | 9.6<br>9.2-10.1              | 8.2<br>7.7-8.5   |
| <i>N. f. riparia</i> , 2 ♀, Vernalis                                       |                             |                          |                          |                                |                                |                                |                                |                    |                  |                       |                            |                          |                           |                              |                  |
| 443.5<br>435-452                                                           | 216<br>215-217              | 43.5<br>43-44            | 31<br>31-31              | 42.0<br>41.8-42.2              | 27.1<br>27.1-27.1              | 19.4<br>18.8-20.0              | 17.25<br>17.2-17.3             | 8.05<br>7.9-8.2    | 8.35<br>8.2-8.5  | 6.0<br>5.7-6.3        | 10.9<br>10.8-11.0          | 9.2<br>8.8-9.6           | 20.0<br>19.5-20.5         | 9.4<br>9.2-9.6               | 8.55<br>8.5-8.6  |
| <i>N. f. perplexa</i> , 5 ♀, Priest Valley                                 |                             |                          |                          |                                |                                |                                |                                |                    |                  |                       |                            |                          |                           |                              |                  |
| 407<br>377-427                                                             | 196<br>184-206              | 39<br>38-41              | 29<br>28-30              | 39.2<br>37.9-40.9              | 25.2<br>24.6-26.0              | 18.5 <sup>a</sup><br>18.0-18.8 | 16.4<br>16.1-16.7              | 7.5<br>7.3-7.7     | 7.8<br>7.3-8.4   | 5.8<br>5.7-6.0        | 10.2<br>9.6-11.0           | 8.5<br>8.2-8.9           | 18.7<br>18.0-19.4         | 9.4<br>8.9-9.7               | 8.6<br>8.3-8.7   |

*N. f. bullator*, 3 ♀ ♀, San Miguel

|         |         |       |       |           |           |           |           |         |         |         |           |         |           |         |         |
|---------|---------|-------|-------|-----------|-----------|-----------|-----------|---------|---------|---------|-----------|---------|-----------|---------|---------|
| 441     | 218     | 42    | 34    | 42.1      | 26.2      | 19.0      | 17.6      | 7.8     | 8.0     | 6.0     | 10.7      | 9.6     | 20.3      | 9.7     | 8.8     |
| 439-445 | 214-221 | 40-44 | 33-35 | 41.5-43.3 | 25.5-27.0 | 18.7-19.4 | 17.5-17.8 | 7.8-7.9 | 7.8-8.3 | 5.9-6.1 | 10.7-10.8 | 9.4-9.8 | 20.2-20.5 | 9.6-9.8 | 8.6-9.0 |

*N. f. streator*, 8 ♀ ♀, Carbondale

|                  |                  |                 |       |           |                   |                   |           |                  |                  |                  |          |         |           |         |         |
|------------------|------------------|-----------------|-------|-----------|-------------------|-------------------|-----------|------------------|------------------|------------------|----------|---------|-----------|---------|---------|
| 378 <sup>r</sup> | 187 <sup>r</sup> | 39 <sup>r</sup> | 26    | 37.9      | 23.8 <sup>r</sup> | 17.6 <sup>r</sup> | 15.7      | 7.0 <sup>r</sup> | 7.3 <sup>r</sup> | 5.8 <sup>r</sup> | 10.0     | 8.0     | 18.0      | 9.0     | 7.4     |
| 360-394          | 180-197          | 38-40           | 24-27 | 36.7-39.1 | 23.1-24.3         | 16.7-18.6         | 15.3-16.1 | 6.4-7.3          | 7.0-7.5          | 5.4-6.2          | 9.4-10.4 | 7.5-8.3 | 17.2-18.5 | 8.6-9.3 | 7.1-7.7 |

*N. f. macrotis*, 5 ♀ ♀, San Diego

|                  |                  |                 |       |                   |           |           |                   |         |         |         |          |         |           |         |         |
|------------------|------------------|-----------------|-------|-------------------|-----------|-----------|-------------------|---------|---------|---------|----------|---------|-----------|---------|---------|
| 368 <sup>a</sup> | 175 <sup>a</sup> | 37 <sup>a</sup> | 27    | 37.5 <sup>a</sup> | 22.6      | 18.3      | 15.4 <sup>a</sup> | 6.6     | 7.1     | 5.5     | 9.7      | 7.7     | 17.5      | 8.8     | 7.6     |
| 363-372          | 165-181          | 36-37           | 26-28 | 37.0-38.2         | 21.8-23.6 | 17.7-19.0 | 14.9-15.7         | 6.3-7.0 | 6.8-7.5 | 5.3-6.1 | 9.1-10.4 | 7.5-7.9 | 16.8-18.2 | 8.5-9.3 | 7.4-7.7 |

*N. f. simplex*, 4 ♀ ♀, San Emigdio Creek

|         |         |       |       |           |           |           |           |         |         |         |         |         |           |         |         |
|---------|---------|-------|-------|-----------|-----------|-----------|-----------|---------|---------|---------|---------|---------|-----------|---------|---------|
| 400     | 187     | 37    | 27    | 38.5      | 24.7      | 18.6      | 15.8      | 7.2     | 6.9     | 5.3     | 9.7     | 8.4     | 18.1      | 9.1     | 7.8     |
| 390-409 | 180-190 | 37-37 | 27-27 | 38.0-39.3 | 24.5-24.9 | 18.0-19.2 | 15.2-16.3 | 7.0-7.5 | 6.9-7.2 | 5.0-5.6 | 9.3-9.9 | 8.1-8.8 | 17.7-18.7 | 9.0-9.3 | 7.5-8.0 |

*N. f. luciana*, 4 ♀ ♀, Seaside

|         |         |       |       |           |                   |           |                   |         |         |         |          |         |           |          |         |
|---------|---------|-------|-------|-----------|-------------------|-----------|-------------------|---------|---------|---------|----------|---------|-----------|----------|---------|
| 393     | 196     | 40.5  | 27    | 38.7      | 24.3 <sup>s</sup> | 18.2      | 16.2 <sup>s</sup> | 7.3     | 7.5     | 5.7     | 10.2     | 8.3     | 18.6      | 9.8      | 7.9     |
| 380-408 | 189-202 | 40-41 | 26-28 | 37.6-39.6 | 24.0-24.5         | 17.8-18.5 | 15.8-16.8         | 7.1-7.5 | 7.3-7.6 | 5.3-6.5 | 9.5-10.7 | 8.0-8.7 | 18.2-18.7 | 9.3-10.3 | 7.6-8.2 |

*N. f. martirensis*, 5 ♀ ♀, Sierra San Pedro Mártir

|         |         |       |       |                   |           |           |                   |         |         |         |          |         |           |         |         |
|---------|---------|-------|-------|-------------------|-----------|-----------|-------------------|---------|---------|---------|----------|---------|-----------|---------|---------|
| 354     | 167     | 35    | 28    | 37.1 <sup>a</sup> | 22.8      | 17.1      | 15.3 <sup>a</sup> | 6.6     | 6.7     | 5.5     | 9.4      | 7.9     | 17.3      | 8.4     | 7.4     |
| 335-363 | 160-170 | 34-35 | 27-30 | 36.3-37.8         | 22.3-23.1 | 16.2-17.6 | 14.4-15.9         | 6.1-6.9 | 6.5-7.1 | 5.3-5.7 | 8.9-10.1 | 7.5-8.3 | 16.6-17.9 | 8.0-8.6 | 7.2-7.6 |

TABLE 2  
AVERAGE AND EXTREME MEASUREMENTS IN MILLIMETERS OF ADULT MALES OF ELEVEN SUBSPECIES OF *Neotoma fuscipes*  
(Key numbers indicate number of specimens examined if fewer than that indicated by subspecies headings)

| Total length                                                                | Tail vertebrae              | Hind foot                | Ear, from anterior notch   | Basilar length    | Zygomatic breadth | Length of nasals               | Depth of skull                 | Breadth of rostrum | Depth of rostrum            | Inter-orbital breadth | Length of incisive foramen | Length of palatal bridge | Sum of foramen and bridge | Length of upper-molar series | Breadth of bulla |
|-----------------------------------------------------------------------------|-----------------------------|--------------------------|----------------------------|-------------------|-------------------|--------------------------------|--------------------------------|--------------------|-----------------------------|-----------------------|----------------------------|--------------------------|---------------------------|------------------------------|------------------|
| <i>N. f. monochrousa</i> , 7 ♂♂, 7 mi. W Cazadero                           |                             |                          |                            |                   |                   |                                |                                |                    |                             |                       |                            |                          |                           |                              |                  |
| 431<br>185-450                                                              | 204<br>185-216              | 41<br>39-42              | 25<br>24-25                | 41.3<br>39.6-42.3 | 25.6<br>24.2-27.0 | 18.9<br>18.2-19.7              | 16.3<br>15.5-16.8              | 7.5<br>7.1-8.1     | 7.6<br>7.2-7.9              | 6.0<br>5.7-6.3        | 10.5<br>10.1-10.9          | 9.4<br>8.7-10.1          | 19.9<br>19.6-20.7         | 9.7<br>9.1-10.1              | 7.9<br>7.7-8.5   |
| <i>N. f. fuscipes</i> , 6 ♂♂, Yolo and Glenn counties                       |                             |                          |                            |                   |                   |                                |                                |                    |                             |                       |                            |                          |                           |                              |                  |
| 405<br>381-432                                                              | 192<br>182-204              | 40<br>38-41              | 26<br>24-29                | 40.6<br>39.0-42.3 | 25.5<br>24.9-26.6 | 19.0<br>18.5-20.2              | 16.7<br>16.3-16.9              | 7.3<br>7.1-7.6     | 7.6<br>7.4-7.9              | 5.9<br>5.7-6.3        | 10.2<br>9.5-10.8           | 9.0<br>8.0-9.8           | 19.2<br>17.9-20.2         | 9.5<br>9.2-10.0              | 7.9<br>7.8-8.2   |
| <i>N. f. annectens</i> , 7 ♂♂, San Mateo and (western) Santa Clara counties |                             |                          |                            |                   |                   |                                |                                |                    |                             |                       |                            |                          |                           |                              |                  |
| 427 <sup>4</sup><br>412-453                                                 | 210 <sup>4</sup><br>201-226 | 44 <sup>4</sup><br>41-47 | 27.5 <sup>4</sup><br>27-28 | 41.5<br>40.6-42.5 | 26.5<br>25.5-28.1 | 19.0 <sup>6</sup><br>18.1-19.7 | 17.0 <sup>6</sup><br>17.8-19.0 | 7.8<br>7.4-8.3     | 8.1 <sup>6</sup><br>7.6-8.7 | 5.9<br>5.4-6.2        | 10.6<br>10.2-11.2          | 9.6<br>9.3-10.0          | 20.3<br>19.8-20.6         | 9.8<br>9.3-10.3              | 8.2<br>7.6-8.7   |
| <i>N. f. riparia</i> , 3 ♂♂, Vernalis                                       |                             |                          |                            |                   |                   |                                |                                |                    |                             |                       |                            |                          |                           |                              |                  |
| 443<br>434-448                                                              | 217<br>207-224              | 44<br>44-45              | 32<br>31-33                | 42.1<br>40.0-44.7 | 26.4<br>25.6-27.3 | 20.0<br>19.3-21.4              | 17.1<br>16.6-17.4              | 8.1<br>8.0-8.1     | 8.5<br>8.2-8.7              | 6.3<br>6.1-6.6        | 10.6<br>10.1-11.0          | 9.2<br>8.8-9.7           | 19.7<br>19.1-20.5         | 9.8<br>9.7-9.9               | 8.2<br>8.1-8.3   |
| <i>N. f. perplexa</i> , 4 ♂♂, Priest Valley                                 |                             |                          |                            |                   |                   |                                |                                |                    |                             |                       |                            |                          |                           |                              |                  |
| 419<br>404-442                                                              | 198<br>186-206              | 40<br>39-41              | 29<br>28-30                | 40.3<br>39.3-41.6 | 25.7<br>25.2-26.2 | 19.3<br>18.6-20.3              | 16.7<br>16.4-17.2              | 7.7<br>7.5-7.9     | 8.1<br>7.7-8.3              | 5.9<br>5.7-6.1        | 10.0<br>9.6-10.1           | 8.9<br>8.4-9.6           | 18.8<br>18.0-19.8         | 9.5<br>9.2-9.7               | 8.2<br>8.1-8.4   |

*N. f. bullator*, 4 ♂♂, San Miguel

|         |         |       |       |           |           |           |                   |         |         |         |           |         |           |         |         |
|---------|---------|-------|-------|-----------|-----------|-----------|-------------------|---------|---------|---------|-----------|---------|-----------|---------|---------|
| 445     | 208     | 43    | 33    | 43.3      | 26.5      | 19.6      | 17.4 <sup>a</sup> | 7.8     | 8.1     | 6.0     | 11.0      | 9.4     | 20.4      | 9.7     | 8.8     |
| 425-468 | 193-226 | 40-45 | 32-36 | 42.6-44.0 | 26.3-26.6 | 18.8-20.4 | 18.7-19.1         | 7.6-8.0 | 7.7-8.3 | 5.6-6.4 | 10.3-11.6 | 9.1-9.7 | 19.7-21.0 | 9.5-9.9 | 8.7-9.1 |

*N. f. streator*, 3 ♂♂, near Carbondale

|                  |                    |                   |       |           |           |           |           |         |         |         |          |         |           |         |         |
|------------------|--------------------|-------------------|-------|-----------|-----------|-----------|-----------|---------|---------|---------|----------|---------|-----------|---------|---------|
| 376 <sup>a</sup> | 186.5 <sup>a</sup> | 41.5 <sup>a</sup> | 25    | 38.3      | 23.5      | 17.8      | 16.1      | 7.2     | 7.3     | 5.9     | 10.0     | 8.0     | 18.0      | 9.1     | 7.4     |
| 372-380          | 183-190            | 41-42             | 24-26 | 37.6-38.7 | 23.0-23.9 | 17.6-18.1 | 15.9-16.5 | 6.9-7.5 | 7.1-7.4 | 5.8-6.1 | 9.4-10.4 | 7.8-8.2 | 17.5-18.6 | 8.9-9.4 | 7.1-7.7 |

*N. f. macrotis*, 7 ♂♂, San Diego

|                  |                  |       |       |                   |           |                   |           |         |         |         |           |         |           |         |         |
|------------------|------------------|-------|-------|-------------------|-----------|-------------------|-----------|---------|---------|---------|-----------|---------|-----------|---------|---------|
| 389 <sup>a</sup> | 191 <sup>a</sup> | 38    | 28    | 39.9 <sup>a</sup> | 24.3      | 18.8 <sup>a</sup> | 15.8      | 6.9     | 7.6     | 5.6     | 10.7      | 8.3     | 19.0      | 8.9     | 7.8     |
| 374-403          | 185-199          | 37-39 | 26-29 | 38.5-41.5         | 23.5-25.7 | 18.3-19.4         | 15.5-16.1 | 6.7-7.2 | 7.3-7.8 | 5.4-5.8 | 10.3-11.1 | 7.6-9.0 | 18.1-19.9 | 8.5-9.3 | 7.4-8.0 |

*N. f. simplex*, 3 ♂♂, San Emigdio Creek

|         |                    |       |       |           |           |           |           |         |         |         |          |         |           |         |         |
|---------|--------------------|-------|-------|-----------|-----------|-----------|-----------|---------|---------|---------|----------|---------|-----------|---------|---------|
| 411     | 177.5 <sup>a</sup> | 38    | 29    | 41.3      | 25.5      | 19.7      | 16.3      | 7.3     | 7.6     | 5.6     | 10.6     | 8.6     | 19.2      | 9.2     | 7.7     |
| 408-425 | 175-180            | 37-38 | 28-31 | 40.6-42.4 | 25.1-26.2 | 19.0-20.4 | 15.9-16.7 | 7.1-7.6 | 7.4-8.1 | 5.4-5.8 | 9.9-11.1 | 8.4-8.9 | 18.5-20.0 | 8.8-9.5 | 7.6-7.9 |

*N. f. luciana*, 6 ♂♂, Seaside

|                  |                  |       |       |           |           |           |           |         |         |         |           |         |           |          |         |
|------------------|------------------|-------|-------|-----------|-----------|-----------|-----------|---------|---------|---------|-----------|---------|-----------|----------|---------|
| 402 <sup>a</sup> | 193 <sup>a</sup> | 40    | 27    | 39.9      | 25.1      | 19.4      | 16.2      | 7.6     | 7.7     | 5.7     | 10.7      | 8.4     | 19.1      | 9.9      | 7.7     |
| 391-421          | 183-201          | 39-41 | 25-28 | 38.2-41.6 | 24.4-25.9 | 17.8-20.3 | 15.7-16.8 | 7.2-8.0 | 7.4-7.9 | 5.4-6.1 | 10.3-11.2 | 8.1-8.9 | 18.6-19.6 | 9.8-10.0 | 7.5-8.1 |

*N. f. martirensis*, 8 ♂♂, Sierra San Pedro Mártir

|                  |                  |       |       |           |           |           |                   |         |         |         |          |         |           |         |         |
|------------------|------------------|-------|-------|-----------|-----------|-----------|-------------------|---------|---------|---------|----------|---------|-----------|---------|---------|
| 362 <sup>7</sup> | 168 <sup>7</sup> | 35    | 28    | 37.5      | 23.1      | 17.6      | 15.7 <sup>a</sup> | 6.5     | 6.8     | 5.5     | 9.6      | 7.8     | 17.4      | 8.5     | 7.5     |
| 340-395          | 152-180          | 33-37 | 26-30 | 35.9-38.9 | 21.9-24.4 | 16.1-19.7 | 15.1-16.2         | 6.1-7.1 | 6.5-7.3 | 4.9-5.7 | 9.1-10.0 | 7.4-8.1 | 16.5-18.0 | 7.8-9.0 | 7.2-8.1 |

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## EXPLANATION OF PLATES



## PLATE 7

Dorsal views of the skulls of the subspecies of *Neotoma fuscipes*. All of mean size and proportions and from female specimens. All views natural size.

Fig. a. *Neotoma fuscipes monochroua*, no. 11488; Cuddeback, Humboldt County, California.

Fig. b. *Neotoma fuscipes fuscipes*, no. 13389; Kangaroo Creek, Siskiyou County, California.

Fig. c. *Neotoma fuscipes annectens*, no. 30432; Stevens Creek, Santa Clara County, California.

Fig. d. *Neotoma fuscipes riparia*, no. 55131; Kincaid's Ranch, 2 mi. NE Vernalis, Stanislaus County, California.

Fig. e. *Neotoma fuscipes perplexa*, no. 14079; Sweeney's Ranch, 22 mi. S Los Banos, Merced County, California.

Fig. f. *Neotoma fuscipes bullator*, no. 28902; San Miguel, San Luis Obispo County, California.

Fig. g. *Neotoma fuscipes streator*, no. 93767; Carbondale, Amador County, California.

Fig. h. *Neotoma fuscipes simplex*, no. 28236; San Emigdio Creek, 1500 ft., Kern County, California.

Fig. i. *Neotoma fuscipes luciana*, no. 29325; Seaside, Monterey County, California.

Fig. j. *Neotoma fuscipes macrotis*, no. 3145; San Diego, San Diego County, California.

Fig. k. *Neotoma fuscipes martirensis*, no. 36121; San José, Lower California.



*a*



*b*



*c*



*d*



*e*



*f*



*g*



*h*



*i*



*j*



*k*

## PLATE 8

Ventral views of the skulls of the subspecies of *Neotoma fuscipes*. All of mean size and proportions and from female specimens. All views natural size.

Fig. a. *Neotoma fuscipes monochroua*, no. 11488; Cuddelback, Humboldt County, California.

Fig. b. *Neotoma fuscipes fuscipes*, no. 13389; Kangaroo Creek, Siskiyou County, California.

Fig. c. *Neotoma fuscipes annexens*, no. 30432; Stevens Creek, Santa Clara County, California.

Fig. d. *Neotoma fuscipes riparia*, no. 55131; Kincaid's Ranch, 2 mi. NE Vernalis, Stanislaus County, California.

Fig. e. *Neotoma fuscipes perplexa*, no. 14079; Sweeney's Ranch, 22 mi. S Los Banos, Merced County, California.

Fig. f. *Neotoma fuscipes bullator*, no. 28902; San Miguel, San Luis Obispo County, California.

Fig. g. *Neotoma fuscipes streator*, no. 93767; Carbondale, Amador County, California.

Fig. h. *Neotoma fuscipes simplex*, no. 28236; San Emigdio Creek, 1500 ft., Kern County, California.

Fig. i. *Neotoma fuscipes luciana*, no. 29325; Seaside, Monterey County, California.

Fig. j. *Neotoma fuscipes macrolis*, no. 3145; San Diego, San Diego County, California.

Fig. k. *Neotoma fuscipes marliirensis*, no. 36121; San José, Lower California.



*a*



*b*



*c*



*d*



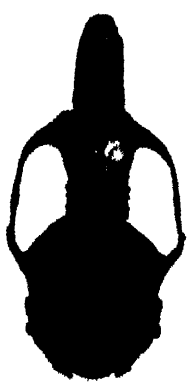
*e*



*f*



*g*



*h*



*i*



*j*



*k*



TERRITORY, ANNUAL CYCLE,  
AND NUMBERS IN A  
POPULATION OF WREN-TITS  
(CHAMAEA FASCIATA)

BY

MARY M. ERICKSON

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# TERRITORY, ANNUAL CYCLE, AND NUMBERS IN A POPULATION OF WREN-TITS (*CHAMAEA* *FASCIATA*)

BY

MARY M. ERICKSON

(Contribution from the University of California Museum of Vertebrate Zoölogy)

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## INTRODUCTION

A KNOWLEDGE of the behavior of a species as seen by a field naturalist—what C. Lloyd Morgan has called the “plain tale”—is basic to an understanding of the physiology and psychology of the individual on the one hand, and of the origin and distribution of the species itself on the other. At the time the present investigation was undertaken, the behavior pattern of few avian species was known in any completeness, and the only worker to attempt to correlate the three fields of behavior, physiology, and psychology, each in the light of the others, was, and indeed is, Eliot Howard. Since his conclusions were based largely on the study of migratory or winter-flocking species, it seemed worth while to study a strictly resident, nonflocking species.

The bird selected for study was the Intermediate Wren-tit, *Chamaea fasciata fasciata* (Gambel). It was believed to possess, to an unusual degree, the habit of fixed residence. The continuity and relative uniformity of its chaparral habitat promised to simplify territorial investigations. The density of population offered vital statistics of fair magnitude within a small workable area. Structural adaptations were obviously correlated with narrowly specialized surroundings. To understand their significance and efficiency was to understand the habits of the bird. The present study has no bearing on the systematic problem of the monotypic family, Chamaeidae, but should form a basis for the study of the five races of *Chamaea fasciata*, especially with respect to the factors which control their distributions. The work reported amounts to a study of Morgan’s “plain tale” with special reference to Howard’s interpretation of it.

The work has been carried on under the guidance of Professor Joseph Grinnell, to whom I am indebted for supervision and criticism. Thanks are also due to the Western Bird-banding Association, which made trapping on a large scale possible, and to Mr. T. T. McCabe for criticism of the manuscript.

## LOCALITY

The field work was carried on in the Berkeley Hills just east and southeast of the University of California campus. These hills, which rise steeply from the bay shelf on which the city of Berkeley and the lower campus are situated, are covered with grass and the canyons are filled with chaparral and with native trees such as coast live oak and California laurel.

A small part of one of the larger canyons called Strawberry Canyon was

used for a preliminary study of three nesting pairs of wren-tits in 1930. In the three succeeding years, an intensive study was made in Hamilton Gulch, a small steep-sided canyon just over the south ridge of Strawberry Canyon with drainage parallel to it. The relation of this gulch to Strawberry Canyon and the general nature of the terrain are shown in plates 9 and 10. The greatest width of Hamilton Gulch from spur to spur is a quarter of a mile, and the distance down through the chaparral from the top of the canyon to the first clearing is a third of a mile. The elevation at this last-mentioned point is 600 feet. From here the spurs on either side rise abruptly to 850 feet, and then converge and unite at 1200 feet. Along the bottom of the canyon, from the mouth to an elevation of about 900 feet, is a small gully which is usually dry but contains running water for a few days at the end of a rainy period. On the lower slopes a narrow footpath has been cleared across the canyon, and starting about on the 820-foot contour on the north slope a road has been cut across the canyon which doubles back and ends about on the 980-foot contour. This, until recleared in the spring of 1932 for a fire road, was so overgrown as to be little more than a trail. At one time the gulch was surveyed for subdivision, but only an occasional stake remains as evidence of this venture.

The plant cover of the gulch is chiefly chaparral; this gives way to grass on the more exposed ridges and to coast live oaks and California laurels in the lower gully. The chaparral, which covers 16.7 acres, is dominated by *Baccharis pilularis*. Other components vary with the exposure and drainage, so that three divisions may be recognized. One prevails on the steep south-facing slope, which drains rapidly and receives the direct rays of the sun most of the day. Here xerophytic conditions exist; the baccharis is relatively open or even sparse, and is mixed with *Artemisia californica*, *Diplacus aurantiacus*, *Rhus diversiloba*, and other plants less conspicuous in size or abundance. On the more protected and less steep north and northwest exposures the baccharis occurs in dense stands and is mixed with *Rhus diversiloba*. The third division occupies the drainage level and parts of the south slope. It represents the most mesophytic condition in the gulch and consists of dense tangles of poison oak (*Rhus diversiloba*) with some elderberry (*Sambucus glauca*) and patches of snowberry (*Symphoricarpos albus*), cream bush (*Holodiscus discolor*), hazelnut (*Corylus rostrata*), wild rose (*Rosa gymnocarpa*), thimbleberry (*Rubus parviflorus*), and blackberry (*Rubus vitifolius*) mixed in varying proportions.

The chaparral, as shown in plates 9 and 10, is cut off completely from any similar area by the grass of the naked ridges and by the trees along the north ridge and in the mouth of the canyon. These barriers suffice to prevent casual movement in and out of the canyon by the wren-tit, and made possible the study of an isolated population.

#### TRAPPING

Extensive trapping was carried on to determine the number of wren-tits present and to mark the individuals so that they could be distinguished.

The traps used at first were of the two- or four-door Potter trap type; but a modification of this, the Western Bird-banding Association two-compartment

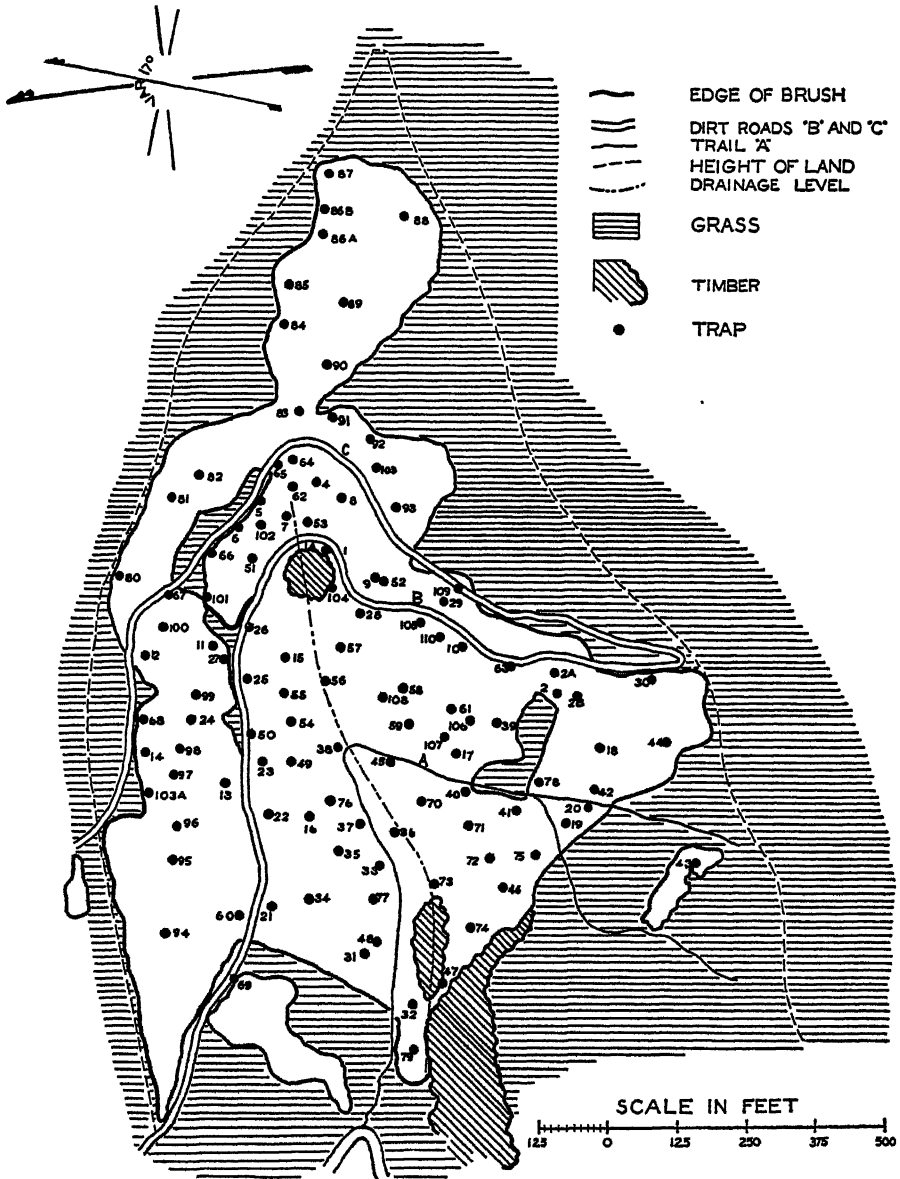


Fig. 1. Index map of Hamilton Gulch, showing trap sites. Map based upon an independent survey.

trap, was used most of the time. The traps were placed on the ground in a clump of bushes in such a way as to have twigs close above and on one or more sides, yet leave the trap visible for a distance of ten feet or more.

A total of 110 trap sites were established. This brought them near enough together to insure taking all the wren-tits and to demonstrate the areas covered by the individuals. The locations of the sites are shown in figure 1. Commonly, a line of thirty or forty were set out in one section of the canyon and

the line run every two hours for six or seven days during a period of about two weeks, when the traps were shifted to a new line. In the three years, a total of eighty-five days were spent trapping.

During the fall and winter, the traps were baited with crumbs of stale but not dry bread scattered only in the compartments. In the summer, small glass dishes filled with water were used as bait. The birds were easily trapped from November to early March, but were hard to catch at other times. If the canyon had not been without water after the rainy season, few birds could have been caught in the summer. From August to September, immature birds were often taken, adults rarely. By such means, and by banding nestlings, which accounted for 48, a total of 180 individual wren-tits were banded. These included all the breeding wren-tits and a large number of the wandering immature birds.

#### MARKING

Each individual was marked with a Biological Survey's numbered metal band and a combination of colored celluloid bands so that it could be recognized at sight.

The bands were made as suggested by Butts (1930), with certain variations. A pair of pliers bored for Number 1 bands as described on page 78 of the *Manual for Bird Banders* (Lincoln and Baldwin, 1929) was used to hold and shape the bands. Celluloid of the right weight and good colors was found in commercial eyeshades. Tall bands, eight millimeters high, made identification easier and could be used on the wren-tit's long tarsus.

At first, the combinations and numbers of bands recommended by Butts were used. Later, the birds were marked by a system using the possible combinations of two colored bands with a Biological Survey band when all three bands were on the same leg, as, for example, a B. S. band on the right leg with a red band above and a yellow one below, or when the two colored bands were on one leg and the B. S. band on the other, as, for example, a red band above a yellow on the right tarsus and a B. S. band on the left. The use of the same number of colored bands on all birds reveals the loss of one and eliminates the danger of misidentification from the rest. Furthermore, putting all the colored bands on one leg is helpful, with wren-tits, because the difficulty of making out marks on both legs is surprisingly great. With six colors, this system provides 240 combinations simple enough for accurate recognition. The colors most easily recognized in the varying lights and shadows were red, yellow, and pink. Green, blue, and lavender were usable, but were much harder to "spot."

Besides, a small spot of color was painted on the tail of each bird of a pair to facilitate recognition of the individual that was incubating. Artist's oil colors diluted with carbon tetrachloride were used and the spot made by touching a brush to the tail while the bird was sitting on the nest.

## DETERMINATION OF SEX

The sexes cannot be distinguished by external appearance, but certain differences in behavior are constant, such as the regular use of the full song by one sex and not by the other. The member of pair XI which did not sing was accidentally killed in a mousetrap and on dissection proved to be a female. This criterion was not checked again by taking any of the birds in Hamilton Gulch, but the sex of two caged birds was correctly assigned on this basis.

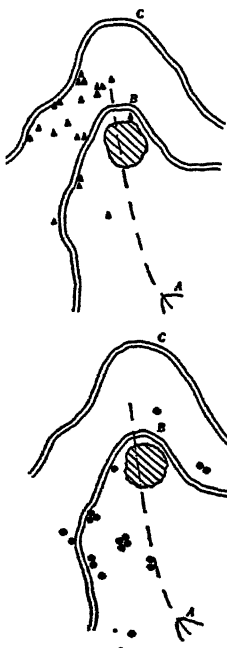


Fig. 2

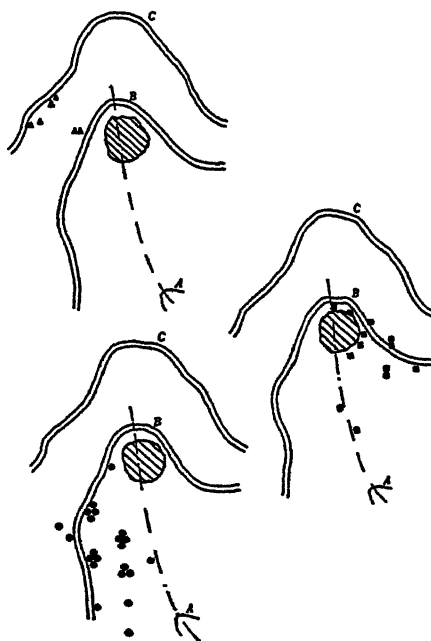


Fig. 3

Fig. 2. Trap records and sight identifications of three males which occupied the section of the canyon along the gully above and below road B. Dot, C41359; square, F21985; triangle, F17812.

Fig. 3. Trap records and sight identifications of three females which occupied the same region as shown in figure 2. Dot, C41362; square, C41353; triangle, F21989.

## TERRITORY

## "THE MATTER OF FACT"

Because the conclusions of Howard concerning territory have recently aroused a more or less skeptical response, I have tried, so far as possible, to present the facts bearing on this phase of behavior as they were accumulated in the field. The most striking fact brought out by the maps in figure 2 is that, during three years of field work, each of the three males was regularly found only in a restricted region of the canyon, and, with the exception of slight overlapping at the margins and the taking of male F17812 in the area of male C41359 once, was not found in the area of an adjoining male. The record for the females, figure 3, indicates that mutually exclusive occupation of restricted areas is

characteristic of this sex also. Equally clearly, a comparison of the two maps shows that only one male and one female were found in the same area, and the obvious conclusion that they were mates was borne out by observation.

Before presenting facts which bear on the nature and degree of this restriction in the various seasons, a brief account of one pair will illustrate the technique used throughout in tracing and plotting the movements of individual birds.

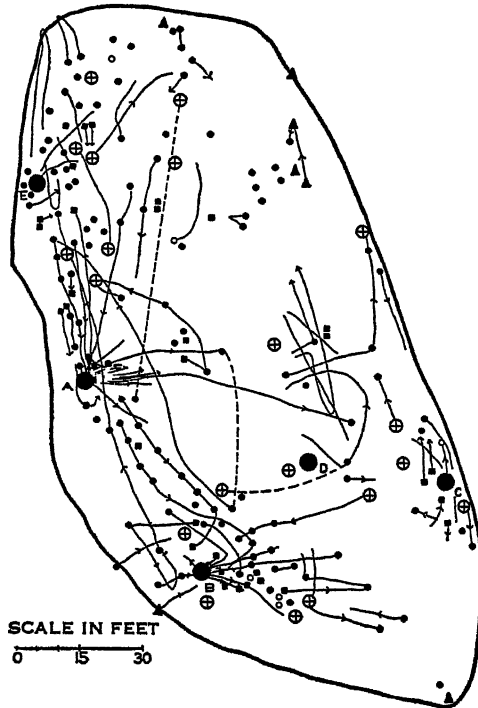


Fig. 4. Observed activities of pair XIX during the breeding season of 1932; 56 hours of observation. Large round spot, nest; small round spot, song by male; small open circle, call by female; large crossed circle, scolding a jay; small square spot, *krring*; triangular spot, fight with intruding wren-tit; continuous fine line, general route taken by wren-tit; broken fine line, went between two points, exact route not known; heavy line, territory boundary.

The records obtained during the breeding season of 1932 for pair XIX, which was rarely trapped but frequently observed, are plotted in figure 4. When first observed early in March, these two were regularly seen together or heard to exchange location notes. The male sang frequently from many different points, at this time and throughout the breeding season. During the second and third weeks of April their activity centered around the first nest at A. Following the loss of this nest, a new one, B, was built, during the last of April, and eggs laid the first days of May. Upon the loss of this set, a third nest was built, at C. The eggs laid in this nest disappeared on the day the third

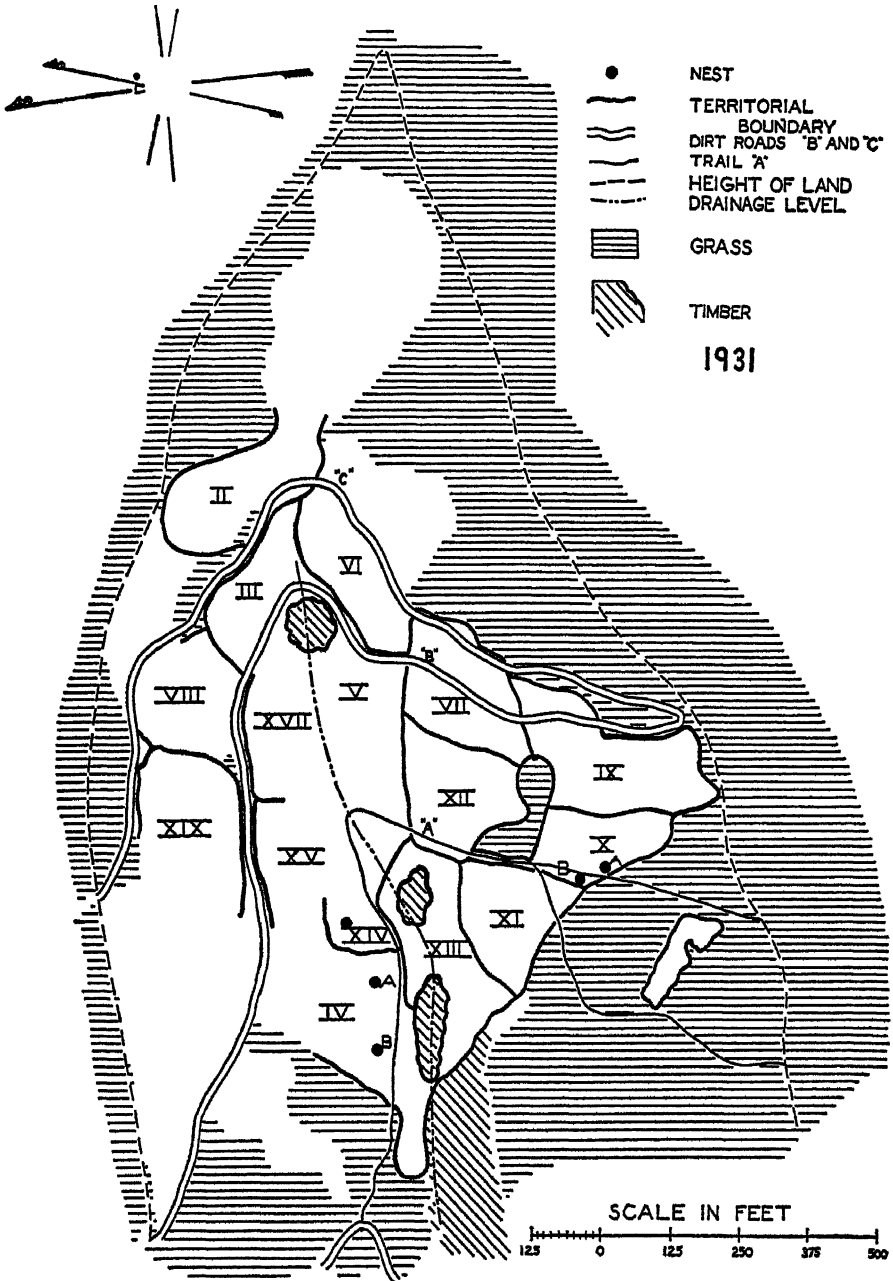


Fig. 5. Wren-tit territories in Hamilton Gulch during 1931. In this year the territorial boundaries were not completely known.



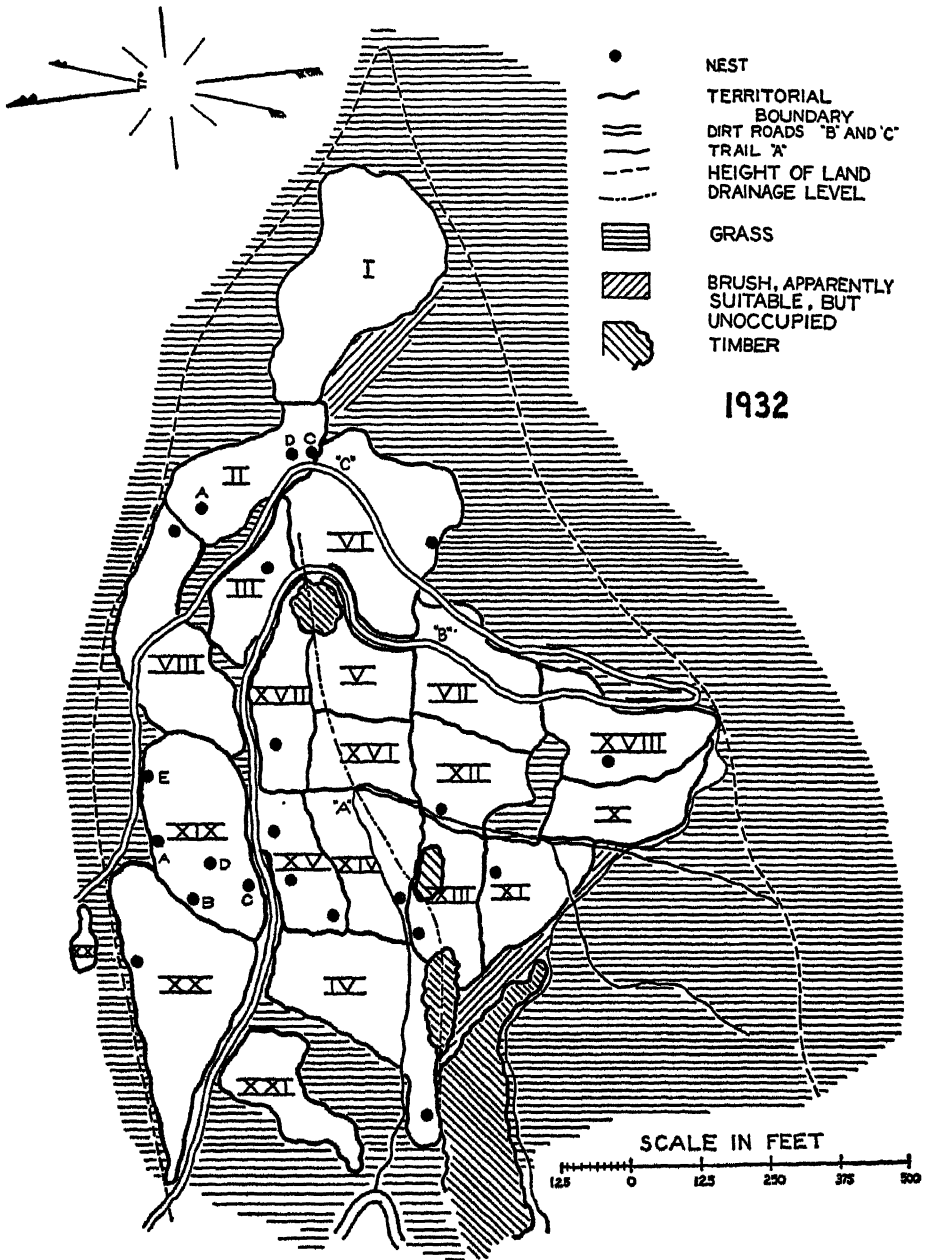


Fig. 6. Wren-tit territories in Hamilton Gulch during 1932.

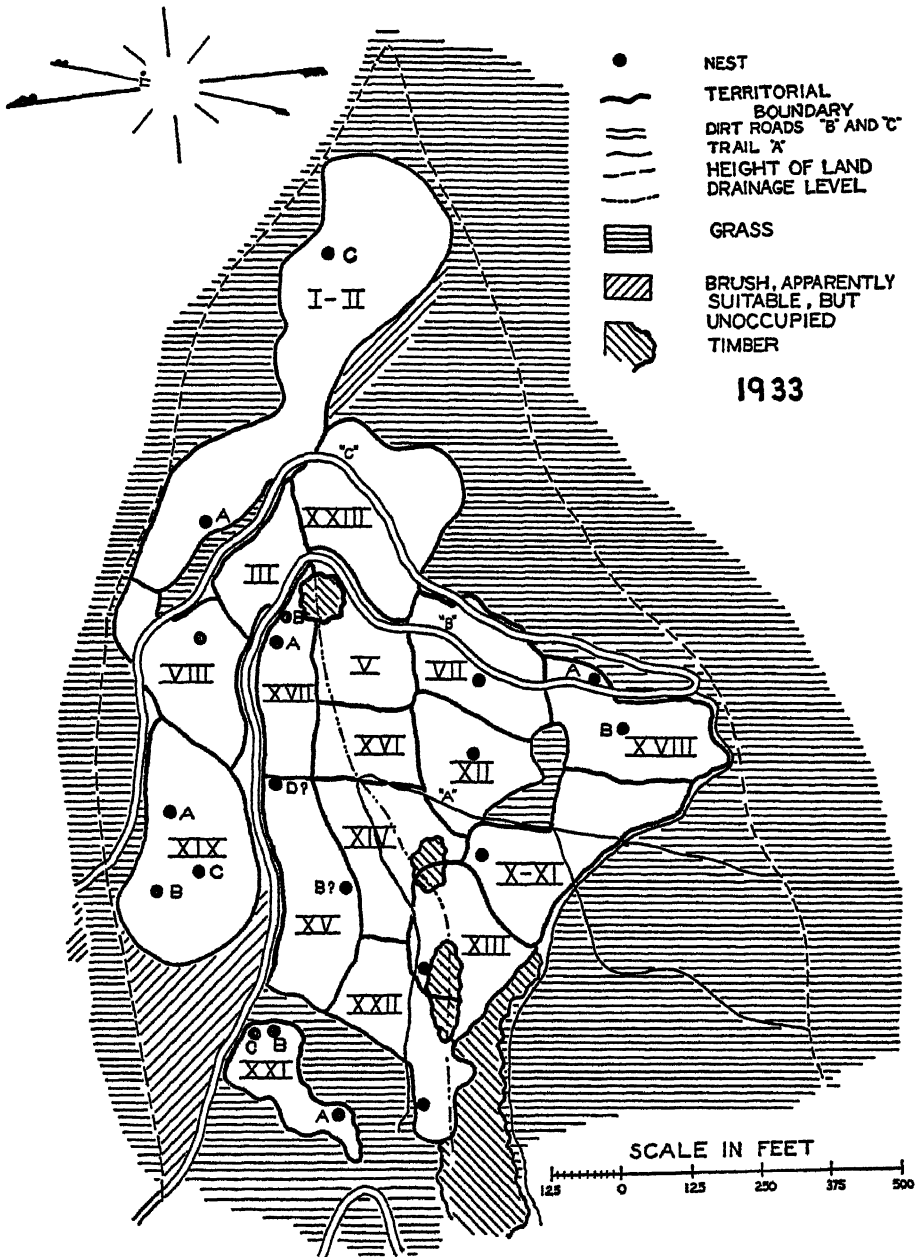


Fig. 7. Wren-tit territories in Hamilton Gulch during 1933.









was laid. By the middle of May, another new nest was constructed, at D, but no eggs were laid. Another was built, at E, and eggs laid in the last days of May, but again the set was lost soon after incubation commenced. So far as known, this was the last attempt to raise young.

In the course of these nesting activities, certain facts became apparent. All the foraging and collecting of nesting material was done within a limited area which included the nest sites. A jay calling fifty feet west of nest B was not mobbed by this pair even when nest B was the one in use, but a jay near nest C was scolded vigorously even before this nest was constructed and after it was abandoned. If the jay moved from this point to the north, east, or west, the pair followed for a longer or shorter distance, still scolding, but if it flew to the south below the road, the pair paid it no further attention.

On June 8, about fifty feet south of trap 24, pair XIX met another wren-tit. Immediately, a battle was fought, in the course of which the birds moved through the brush to a spot about thirty feet east of the starting point. Here the fighting ceased. Nothing more was seen of the alien wren-tit, but male XIX sang repeatedly from a bush a little north of the line of fighting. At other points, pair XIX encountered wren-tits which belonged to one or another of the three adjoining pairs. At each encounter, a fight took place back and forth across or along what appeared to be a region of border warfare, following the same limits that the birds observed in foraging, gathering nesting material, or in pursuit of the jays. When I attempted to drive the pair beyond these limits, the two birds invariably turned back past me.

By repeated observations of this sort, it became clear that at this time pair XIX limited its movements to a section of the canyon about one acre in extent and would not let other wren-tits enter unopposed. The approximate limits of this area are sketched in on figure 4.

After the breeding season, individuals or pairs become difficult to follow and no equally detailed record of one pair is available. In general, the same methods were used in studying the nature and range of movement at this time, but the difficulty of observing individuals and the availability of trap records shifted the emphasis to the latter.

Observations like those already described for a single pair were obtained for most of the breeding pairs during the first year and for all the pairs the last two years. During each of the breeding seasons, the members of each pair were found to restrict their movements to a small part of the canyon. These areas, or territories, were mutually exclusive, but abutted and interlocked so that all the suitable habitat in the canyon was claimed by one pair or another. At points of frequent contact between pairs, the divisions between the territories could be precisely located. If any member of two adjoining pairs chanced to go into a particular bush or to cross a foot or two of open ground between two brush clumps, a boundary dispute between the two pairs invariably followed within a few minutes. In other places, either the observations were insufficient to show the precise limits or the boundary was in the nature of a marginal strip, from a few feet to 15 or 20 feet in width, in which a pair turned back when foraging

or pursuing a jay, and within which it attacked any alien wren-tit. The limits of the territories during the three breeding seasons are represented in figures 5, 6, and 7 by heavy lines. To complete them, it was sometimes necessary to depend on observations of a single pair or to interpolate between known points.

The observations from which these breeding areas were worked out, as well as the records for the fall and winter, are shown graphically in figure 8 and summarized in table 1.

In figure 8 the vertical columns indicate time; the horizontal lines, the span of time for which any sort of record for the individual is available; the type of line, the territorial status of the bird—solid if the bird was occupying a territory, dotted if it was without a territory, broken if it was probably on a territory, dot and dash if the territorial status is uncertain. The solid vertical lines above the horizontal ones indicate days on which the individual was trapped; the broken vertical lines, days on which sight identifications were made. A cross line on either of these represents an additional record on the same day. (With respect to sight identifications, only one is counted if a number were made in the course of an hour or more of continuous observation.) A dot above either indicates that the bird was beyond the margins of its territory. The vertical lines below the horizontal ones stand for days on which the bird was noted on its territory, but in which the identity of the individual is based on the sighting of only part of the band combination and the bird's behavior in relation to the territory, or on its relation to a completely identified mate or to a nest.

Table 1 gives a summary of trap records and sight identifications in relation to territory. The records have been grouped into four categories. The first two groups include records on the territory: number one, the record of birds which were clearly within the breeding territory, and number two, the record of birds that were on the margin of the territory in the region of border warfare. The last two groups include the record of birds which were beyond the usual limits of their movement during the breeding season: number three the record of birds which had gone a short distance into the territory of the next pair, number four the record of birds in which the individual appeared to have abandoned its territory temporarily and was wandering indiscriminately in the canyon. The four groups, of course, are not entirely distinct. Certain records are intermediate and have been put into one group or another on the basis of observations made at the time, or, if trap records, on the basis of general knowledge of the pair.

These records show that 306 identifications were made from the middle of March to the last of July, which is the breeding season, and that no individual was observed outside its boundaries. The total, 306, includes only the trap records and complete sight identifications and excludes the many more records of individuals seen on their territories, but here disregarded because only part of the combination of bands was seen, or because the identity of the individual was based on its relation to a completely identified mate or to a nest. Of 1350 records of this latter sort, only two were of birds which went beyond the usual margins of their territories.



TABLE 1

## SUMMARY OF TRAP RECORDS AND SIGHT IDENTIFICATIONS IN RELATION TO TERRITORY

|                  | 1   | 2  | 3  | 4  | Total | Per-<br>centage<br>1 | Per-<br>centage<br>2 | Per-<br>centage<br>3 | Per-<br>centage<br>4 |
|------------------|-----|----|----|----|-------|----------------------|----------------------|----------------------|----------------------|
| MALES            |     |    |    |    |       |                      |                      |                      |                      |
| March 15-31..... | 13  | 8  | .. | .. | 21    | 61.91                | 38.09                | .....                | .....                |
| April.....       | 16  | 7  | .. | .. | 23    | 69.57                | 30.43                | .....                | .....                |
| May.....         | 56  | 9  | .. | .. | 65    | 86.15                | 13.85                | .....                | .....                |
| June.....        | 49  | 10 | .. | .. | 59    | 83.05                | 16.95                | .....                | .....                |
| July.....        | 9   | 1  | .. | .. | 10    | 90.00                | 10.00                | .....                | .....                |
| Total.....       | 143 | 35 | .. | .. | 178   | 80.33                | 19.67                | .....                | .....                |
| August.....      | 3   | 2  | .. | .. | 5     | 60.00                | 40.00                | .....                | .....                |
| September.....   | 8   | 3  | 3  | .. | 14    | 57.14                | 21.43                | 21.43                | .....                |
| October.....     | 2   | 2  | 1  | 1  | 6     | 33.33                | 33.33                | 16.67                | 16.67                |
| November.....    | 5   | 4  | .. | 1  | 10    | 50.00                | 40.00                | .....                | 10.00                |
| December.....    | 13  | 3  | 2  | .. | 18    | 72.22                | 16.67                | 11.11                | .....                |
| January.....     | 41  | 13 | 9  | .. | 63    | 65.08                | 20.63                | 14.29                | .....                |
| February.....    | 43  | 26 | 5  | .. | 74    | 58.11                | 35.13                | 6.76                 | .....                |
| March 1-14.....  | 22  | 4  | 2  | .. | 28    | 78.57                | 14.29                | 7.15                 | .....                |
| Total.....       | 137 | 57 | 22 | 2  | 218   | 62.85                | 26.15                | 10.09                | .91                  |
| Grand total..... | 280 | 92 | 22 | 2  | 396   | 70.71                | 23.48                | 5.56                 | .50                  |
| FEMALES          |     |    |    |    |       |                      |                      |                      |                      |
| March 15-31..... | 8   | 3  | .. | .. | 11    | 72.73                | 27.27                | .....                | .....                |
| April.....       | 14  | 2  | .. | .. | 16    | 87.50                | 12.50                | .....                | .....                |
| May.....         | 49  | 5  | .. | .. | 54    | 90.74                | 9.26                 | .....                | .....                |
| June.....        | 35  | 8  | .. | .. | 43    | 81.40                | 18.60                | .....                | .....                |
| July.....        | 4   | .. | .. | .. | 4     | 100.00               | .....                | .....                | .....                |
| Total.....       | 110 | 18 | .. | .. | 128   | 85.93                | 14.07                | .....                | .....                |
| August.....      | 2   | .. | 2  | .. | 4     | 50.00                | .....                | 50.00                | .....                |
| September.....   | 3   | 1  | .. | .. | 4     | 75.00                | 25.00                | .....                | .....                |
| October.....     | 4   | 2  | 1  | .. | 7     | 57.14                | 28.57                | 14.29                | .....                |
| November.....    | 2   | 1  | 2  | 1  | 6     | 33.33                | 16.67                | 33.33                | 16.67                |
| December.....    | 13  | 3  | 1  | 1  | 18    | 72.22                | 16.66                | 5.56                 | 5.56                 |
| January.....     | 27  | 13 | 4  | .. | 44    | 61.36                | 29.55                | 9.09                 | .....                |
| February.....    | 29  | 15 | 4  | .. | 48    | 60.42                | 31.25                | 8.33                 | .....                |
| March 1-14.....  | 21  | 4  | 3  | .. | 28    | 75.00                | 14.29                | 10.71                | .....                |
| Total.....       | 101 | 39 | 17 | 2  | 159   | 63.52                | 24.53                | 10.69                | 1.26                 |
| Grand total..... | 211 | 57 | 17 | 2  | 287   | 73.52                | 19.86                | 5.92                 | .70                  |

One of these concerns pair x. On May 8, 1932, one of the pair, presumably the male, went seventy-five feet along the south boundary of territory ix while following and scolding a jay. It was at once driven back by male ix. Even in hot pursuit of an enemy this was unusual, for on many similar occasions the pair turned back at the boundary.

In the second exception, which occurred on June 8, 1933, the male of pair iii crossed the upper road and penetrated the western part of territory ii a short distance. It collected food for its young, sang once, and returned quickly to its own territory. The individuals of pair ii were, at this time, building a nest in the eastern part of their territory and probably were not aware of the invasion. Whether aware of the intruder or not, they did not attack.

If two such exceptions were observed, others must have occurred. Yet, the general impression was not of birds continuously exerting pressure or sparing for an opening, but rather of their acceptance of the existing status. Probably the ratio of 306 to 2, or even of 1650 to 2, does not greatly exaggerate the preponderance of time during which the birds are held, by whatever agencies, internal or external, conscious or unconscious, within their curiously definite frontiers.

By the end of July, the picture is confused by numbers of nearly or fully independent and wandering young. Their presence makes the identity of any individual uncertain except as it is trapped or the pattern of colored bands is determined. At the same time, the chances of making positive identifications decrease because of the greater number of birds, the relative conspicuousness of the young in contrast to the molting adults, and the temporary reluctance of the adults to enter traps.

From this time until the middle of March, 393 trap records or sight identifications of adults were obtained. Of these, 350, or 89 per cent, were within the limits of their breeding territories and 43, or 11 per cent, were beyond the margins of territory observed during the breeding season. Apparently the composition as a whole has not changed, but some relaxation in the sharpness of the boundaries or in the rigidity of their observance is evident.

A consideration of the individual records will give clues to the nature and extent of this relaxation.

Of nine identifications made in August (table 1), seven were of birds on their territory. Of the two others, the first one concerned pair xx. On August 1, 1932, the female was seen in the upper part of territory iv. She was driven out by the owners and went into the lower part of xix. Here, she worked toward her own territory, but had a brief dispute with pair xix on the way. Pair xx had fledged its young early in the season and had been free of them for about two weeks. The second occurred on August 3, 1933. The female of pair xix, her young, and an adult whose colored bands, so far as seen, checked with those of her mate, were seen foraging 100 feet or more beyond the usual limits of their territory along the boundary between xvi and xiv, and in an elderberry tree near the bend of the lower trail. The berries, which were just becoming ripe enough to be used by the birds and were not available in their

home area, may have been the loadstone that drew them beyond its limits. After about an hour in this region, they returned to their own territory. No objection was evident, at any time, from the owners of the territories invaded.

Three of the eighteen identifications made in September are of individuals outside of their territory boundaries. Two males are involved. One was trapped in the next territory. The other, male xvii, was twice seen on the boundary between two territories which adjoined its own. On the first occasion, a brief fight took place in which male xvii was involved but the other participants were not identified. On the second, his curiosity was perhaps excited by an immature bird which was squealing vigorously in trap 9 while another immature bird near by was giving a low *peeka* note. Soon after the trapped bird was released, the two immature birds and male xvii were seen close together in the bushes near the trap.

Of the 352 records for established birds during the next five and a half months, 38 are in groups 3 and 4. All are trap records. In about half of the 38, nothing is known of the time the birds spent outside their territories. In others, something of the length of time and frequency of the excursions is known.

Those which bear on the length of time involved in these excursions follow:

Male xvi was taken on his territory one and a half hours before and after he was trapped in the next territory.

Female xxi was taken on the margin of her territory three hours before and after she was taken in the next territory.

Seven males and one female were taken on their own territories on the same day on which they were taken in the next territory.

Naturally, the actual length of time involved could only be determined through ability to record the bird's departure and return. Since trapping cannot do this, these records undoubtedly give an exaggerated impression of the duration of the excursions, and should be taken merely as maxima, their chief value being in the proof of return.

The records do not suffice as an adequate measure of the frequency of these excursions, but the following facts extracted from figure 8 are suggestive.

Pair iv.—Male taken or seen 10 times; all on territory. Female taken 6 times; all on territory.

Pair x.—Male taken 10 times; all on territory. Female taken 7 times; 2 short (in group 3, table 1) excursions.

Pair xi.—Male taken or seen 25 times; 1 short excursion in February of the year it first bred on the territory. Female—three individuals involved: first taken 10 times, all on territory; second taken 4 times, all on territory; third taken 3 times, all on territory. (Third female is female x, which fused her 1932 territory with that of male xi in 1933. One of the short excursions when she was the mate of male x was into territory xi.)

Pair xii.—Male taken 14 times; all on territory. Female (1932) taken 12 times; 1 short excursion.

Pair xiii.—Male taken 8 times; all on territory. Female taken 4 times; all on territory.

Pair xvi.—Male taken 15 times; 3 short excursions. Female taken 5 times; 3 short excursions; present, but status unknown, prior to breeding season of 1932; probably wandering in 1931 or, less likely, shifted her territory in January, 1932; apparently joined male on a territory in February, 1932.

During the time these records were obtained, traps were operated throughout the lower half of the canyon and afforded the possibility of taking these individuals either on their territory or on most excursions from them. No records of long excursions by birds of the upper part of the canyon occurred.

Pair **xxi**.—Male taken 8 times; 1 short, 2 long (group 4, table 1) excursions. Female taken or seen 10 times; 3 short, 1 long excursion. Traps were not being operated in their own territory at the time of the long excursions.

These records suggest that for most individuals short excursions are of infrequent occurrence even in winter. The two pairs **xvi** and **xxi**, for which a larger number of excursions are recorded, both occupied territories in which the plant cover was similar to that found in other territories but which were very small. Perhaps this necessitated foraging over a larger area during the winter, but individual peculiarities in respect to wandering are also a possibility.

The scant material that bears on the part of the interbreeding period in which these excursions are most likely to occur is summarized in table 1, and shows that excursions may be more common from August to October or November than in the months that follow.

Little evidence is available to show whether one sex is more prone to wander than the other. The proportion of excursions by males is higher than that by females in January, and decreases more rapidly in the succeeding months. This may represent the chance distribution of the few excursions recorded, or may shadow forth a real difference in the time and degree of restriction of the males and females.

Within the cycle of a single year, then, a wren-tit's possession of a territory is continuous, but the strictness with which its limits are observed varies somewhat with the season. During the breeding season its observance is absolute. As the breeding season merges into the postbreeding season, in the latter part of July, tolerance of wandering young is shown by the established pairs, and, coincident with this, occasional excursions by the adults, with their young or alone, may not be protested. Through the fall and early winter, short excursions from the territory and, less frequently, excursions of some extent may occur in the course of a day's activity. As early as January, the movements of the pairs become more restricted. No long excursions occur. Short excursions, scarcely beyond the region of border warfare, occur probably as a result of sexual interest or antagonism, but gradually decrease in frequency until, in the last of March, the complete stability of territory characteristic of the breeding season is reached.

Since the individuals retain their territory throughout the year, it is natural to find them occupying the same location in successive years. Sixteen individuals occupied the same territory for three successive years, and one other retained the same territory for three years but disappeared early in the breeding season of the third year. Five individuals were found on the same territory the first two years but had disappeared at the beginning of the third breeding season. Five others were on territories the last two years and were still present at the close of the field work. Nineteen individuals were known

for only one year. Of these, ten were known only during one breeding season but may have been present previously. Five first appeared in 1933 and were still present when field work was discontinued. Four were present for one year only. Seven individuals that bred remain to be considered. One male retained the same territory throughout, but in 1933 fused it with the 1932 territory of his new mate, which likewise extended her territory to include his. Twice more, fusion of estates by marriage was observed. In one of these, each member of the pair had been on the original territory for only one year. In the other, the female had been present only one year, the male at least two.

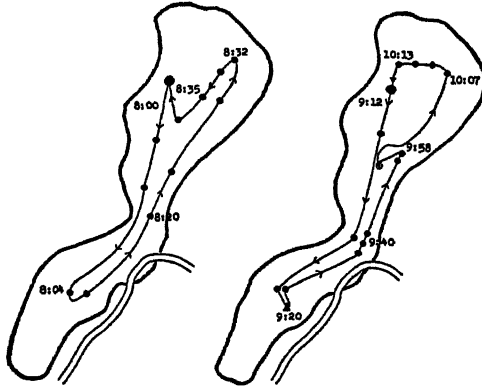


Fig. 9. Movements of male II and the points from which he sang during two intervals away from the nest on June 19, 1933. Large dot, nest; small dot, song; triangle, fight; cross in circle, scolding jay.

The one remaining record is that of a female which occupied the same territory for the first two years, but on the loss of her mate joined another male on his territory and relinquished her own.

Considered in terms of pairs (fig. 8), numbers III, V, VII, VIII, and XV existed unchanged throughout the three years of the study and, as a comparison of figures 5, 6, and 7 shows, their territories were the same except for minor shifts of the boundaries. Another pair, XIV, started the third season together, but was broken up by the loss of the male. Three pairs, IV, VI, and XIII, were together during the first two years, but were broken up by the loss of one or both members. Three others, XVIII, XIX, and XXI, were first known as pairs in 1932 and were unbroken at the end of the field work. Nineteen pairs were known for one year only. Of these, fourteen may have been in existence before the period of the study and may have continued after it. Five lasted for one year only.

When a pair was broken up, one or both members of it disappeared entirely. One female was killed in a mousetrap. The exact fate of the seventeen others that disappeared is unknown, but undoubtedly it was death for most of them if not for all, since all the evidence indicates that the males, if they survived, would be present on their territory, and the females would be on a near-by territory. As I have explained elsewhere, it is almost certain that they did

not cross the barriers which set off the brush of the canyon from other brush areas, the largest of which was consistently trapped by other bird banders. Whenever both individuals of a pair have survived from one breeding season to the next, they have been together on essentially the same territory.

The average number of years that an individual lives and hence retains its territory will be considered later. One individual, a male banded first on March 22, 1925, and taken three times thereafter (September 6 and December 6 and 26, 1925) by E. D. Clabaugh, was retaken at the same place by E. L. Sumner, Sr., on February 3, 1931, and thirteen times subsequently, the last time on February 21, 1934. In 1933, this wren-tit and his mate successfully fledged a brood. Evidently, this individual had retained the same territory from 1925 until 1934, a period of ten years.

#### MAINTENANCE OF TERRITORY

The pair not only remains in the restricted area but also prevents neighboring or errant wren-tits from invading its territory. This end is achieved by the male's proclamation of his presence and possession, and by driving out invaders, a function of both sexes.

As is true of many other small, cover-haunting species, the wren-tit depends on voice rather than display to announce its presence. The utterance is a ringing song, typically composed of a series of whistle-like notes speeded toward the end into a trill, all given on the same pitch and lasting three or four seconds. It has great carrying power and to the human ear is one of the most characteristic sounds of the chaparral. It may be given from the top of a bush or from dead branches where the bird is visible, but comes most often from a perch below the leafy crown where the singer is hard to see. It may be given from any bush within the territory. Slight preference is shown for certain bushes, but none could be referred to as a "singing post."

A few of many commonplace instances of its use are here presented, selected from my field notes:

March 28, 1932, 9:30 A.M.—*Pit-trrr* from baccharis... given repeatedly; no answer; [wren-tit] hopped about on open branches below crown as [it] gave song.

May 6, 1932 [fig. 6], 8:15 A.M.—*Pit-trrr* song given by [male] xv below road B, in dead baccharis 35 feet east of [west boundary]; given several times from this open perch, then bird suddenly flew just above brush to west, disappearing about... [at northwest corner of territory]. In about three minutes call heard again, bird seen in brush... [on boundary], moved [back] to first perch, sang several times and then flew down into brush.

April 3, 1930, 8:45 A.M.—... pair came from oaks into hazel shrub. An [other] individual up the slope gave *pit-trrr* song several times, one of pair... sang twice... one up on slope sang a number of times.

June 8, 1932 [fig. 6].—[*Pit-trrr* song given alternately by males II and VI as follows:] 11:26, II, VI, II, VI, II, VI, II, 11:27. Male II in lower part of territory above road, male VI below road [near center of this section of his territory]. 11:28, two more *pit-trrr* songs from low in territory II; 11:29, four more from about same place; then, 11:32, VI, VI, II, VI, VI, II, VI, 11:33, II, VI, VI, VI, II, VI, II. Male II now 25 to 30 feet northwest of position at 11:26, male VI moving toward northwest corner of his territory. 11:36, three more songs from II above road. 11:37... [dispute at corner of territories II, III, and VI]. 11:41, male of pair II crossed to upper side of road. 11:45, II, VI, VI, II, VI, II, II. Male II in lower part of his territory, others on boundary between VI and III.



territory xx, 10 feet west of point where dispute occurred. [Wren-tit] called repeatedly [while] working . . . [along lower boundary of territory xx], called at intervals of a few seconds . . . [until at least] 4:50, when I left vicinity.

The song is uttered at all times of the year. It is most frequent during the early part of the breeding season and from the last part of August into October, and is least common during November and December. The persistence of the song the year round and even during the molt is characteristic of the species, and has been emphasized by Cooper (1869), Keeler (1890), Grinnell (1913), Hunt (1922), Grinnell and Storer (1924, p. 584), and Smith (1930). If song is a means of announcing the possession of territory, it is to be expected that it would be used throughout the year by a species holding territory continuously, and that it would increase in frequency in the fall, when the young-of-the-year are seeking territories.

The song may function as a specific warning as well as a general proclamation. When male xx sang near the boundary line and within thirty feet of nest xixb, 1932, male xix, which was fifty feet above the nest, sang once, loud, ringingly; and flew toward the nest, head feathers erected. The warning was evidently enough. Nothing more was heard or seen of male xx.

An intruding wren-tit working low through the dense cover is not quickly detected by sight. Invaders of a territory are sometimes detected by their song, but more frequently by their call notes, which stimulate the pair whose frontiers are threatened or crossed. For example, the male of pair xiii was observed near the center of his territory, foraging for and feeding his five-weeks-old young. The male of an adjoining pair sang on the common boundary. Male xiii stopped foraging, sang once, advanced rapidly through the brush toward the point of invasion, disregarding the food calls of his young, paused, sang again, continued his advance and, finally, met and fought briefly with the infringing pair. On another occasion, pair x was seen in the south-central part of its territory. One minute later, at a point where pair x had been seen an hour and a half before, the neighboring pair, xviii, was heard scolding, and the male sang once. Pair x was seen moving rapidly from the southwest toward this point, and a fight ensued. On another occasion, the family of territory vii was foraging north through the brush on the west side of the lower road. As usual, both the young and the adults were uttering frequent location notes. They advanced to the bushes beyond their usual limit of movement, and some entered them. Suddenly a fight took place involving this group and pair v. Then family vii was seen working back to the south along road B. At a point near the center of the territory, they crossed to the upper side of this road and in the course of foraging worked to the northeast toward territory xxiii and the upper road. Again as they reached the boundary a fight took place, this time with pair xxiii. As it ended, the male of family vii retreated toward the center of his territory and the young drifted in the same direction. Such encounters often occurred. The call notes of individuals which are on or moving toward a boundary are recognized as potential invasion, and the threatened pair advances to offer resistance.



Rarely, sight may be the sense by which an intruder is detected. Pair VIII had been watched for an hour feeding a single fledgling. Suddenly, each adult uttered a sharp *ter* and started in rapid pursuit of a single intruder which had been sighted halfway between the youngster and myself. I had been entirely unaware of its presence, though it was less than twenty-five feet away. On another occasion, male XX had been moving from the lower to the upper part of his territory, singing as he moved and at the top singing repeatedly from a clump of bushes near the boundary between XX and XIX. No other birds were observed, but suddenly sounds of a fight were heard at the edge of this clump, and presently I saw the male of XIX return to his territory. A little later he was back, silently collecting grass fiber as he had probably been caught doing before.

The fighting which takes place when an invader is discovered rarely deserves the name. As described for other species, it is formalized, and usually consists of a series of vocal threats and posturing. Except during the incubation period, both members of the pair are involved. When intruders are detected, the defending bird or birds approach to within one to three feet of them. The head feathers are raised, the tail cocked sharply up, the body crouched and tense. Each bird eyes its opponent and shifts its position or perch as if sparring for an opening. One or more may utter a staccato *ter ter ter* or a more continuous *pit' pit' pit'*. This may go on for only a moment or for fifteen or twenty minutes or, on rare occasions, even longer. If it is prolonged, one bird may fly at the other, but the latter makes a quick shift and is a foot or two away when the attacker reaches the empty perch. This continues as the opponents move rapidly through a bush, or along the boundary or back and forth across it. Sometimes the pursuer becomes the pursued. Rarely, the combatants fly at each other and momentarily flutter through the brush or on the ground, bills clicking and wings striking. If the fight lasts many minutes, one or more of the contestants may drop out of active participation and forage or preen; whenever the identity of such an individual has been determined, it has been a female. She may move some yards back into her territory, remain near the disputing males, or be left behind. If the males give the *ter* or *pit* note, she usually adds a *peeka, peeka* call. Eventually one pair, usually the invaders, works back toward the center of its territory and the others soon do likewise. The defending male usually sings, the invader sometimes does.

Most of the fighting takes place along the boundaries in what I have called the region of border warfare. On one occasion, however, a single individual persistently stayed within the territory of an established pair and was as persistently harassed by the owner. My field notes describing parts of the encounter follow:

April 29, 1931 [fig. 5].—... Heard sounds of a dispute, ... two [wren-tits] on north bank [of trail A on north slope], three on lower side. 9:10, ... two of three on lower side flew at each other, ... [a wren-tit] came down from north bank [to point of dispute] ... , went back. All five worked [west] along A ... [100 feet along north boundary of XIII]. Two on north bank seemed to withdraw. Still three below; one continually dives at other; third follows closely or sometimes remains in bush. A number of times one called *peeka peeka*, others

joined with *pit-pit* or *tut-tut*. Two chase rapidly from one perch to next, a scant foot between, going through brush [and] live oaks [in an area of about 1000 sq. ft. near center of territory xiii]; then a brief pause; then chase again. Pursuer seen to forage once during such a pause. . . . [Rapid, almost continuous pursuit until 9:50.] Birds less in evidence from 9:50 until 10:10, then repeated *pit-trrr* song from . . . [near center of territory] and an occasional *pit-pit* answer from . . . [near northwest boundary] . . . , two continued calls. 10:20, saw two in live oak; calls continued. 10:21, calls continued. 10:24, two seen again in pursuit in brush and live oak. Once in oak, pursued one called *pit-pit*, pursuer answered in slightly different tone . . . , [a third] in one of oaks calling *pit-trrr* repeatedly. 10:40, two chased through brush . . . [on north boundary], one in oak still calling *pit-trrr*. 10:40½, two went back into oak, chase very rapid. 10:41, paused in oak momentarily, then at it again. As paused, pursuer called *pit-pit*, . . . [third] bird [which had been calling] in oak called *pit-trrr* immediately, . . . [then went into brush at northwest corner of territory], called *pit-trrr*. *Peeka* chorus by two, came into . . . [brush of northwest corner, within two feet of observer], perching inaccurate, banged into branches; went back without pausing. 11:40, three chased through oaks and brush, two in close pursuit; a third behind slower, not taking all the rapid turns, and stayed in oak. 11:50, seen in chase again; *pit-trrr* and *pit-pit* answer again. 11:51, *pit-trrr* call from oaks; *pit-pit* call . . . [from brush]. 12:05, pursuit still on though birds less frequently seen. About 12:07, after all had been quiet for a time, one wren-tit . . . [near northwest corner] crossed trail A [boundary line] to upper bank, foraged here; lost after a few minutes but did not recross trail A. 12:13, quiet. 12:25, still quiet. [12:30-12:40, observer away from area.] 12:40, still quiet.

This account seems to be the record of an attempt on the part of one wren-tit to carve out a territory in an area already occupied. Since none of the birds was distinctively banded, the relation and sex of the individuals could not be worked out. At the time, I had only heard males give the *pit-trrr* song and wondered if the main fight was between an intruding female and the female owner. Since then, I have identified a female as she gave the full song during a boundary dispute between her mate and a neighboring individual. In view of this, the more probable, or equally probable, explanation is that a male seeking to establish himself was driven out by the established male.

The first record of the detection of an invader by sight likewise had to do with a bird which had reached the center of a territory, but the intruder, probably a young-of-the-year, instantly gave way and left the territory when attacked.

Fighting was observed in *all months of the year*. The disputes were frequent for a month or two just before nest building. During the last of the breeding season they were less common. In the fall they increased in frequency, as did song. My records for December show a drop during this month. This may be chance, for the amount of field work was relatively small, or it may be correlated with the cold, foggy, and windy weather of this month.

During the breeding season, fights occurred between pairs in all stages of the reproductive cycle. Pairs which were building a nest were involved in disputes with pairs in the same stage and with those that were incubating or feeding young. Likewise, disputes took place between pairs that were brooding or feeding young. In the fall, disputes occurred between two established pairs and between established pairs and young-of-the-year.

## ACQUISITION OF TERRITORY

Since a male, once established on a territory, retains it continuously, the search for territory by members of this sex is limited to the young birds. The female acquires a territory secondarily through her mate, so that of this sex either a young bird or an adult whose mate has been lost may be involved. The remating of a widowed female has already been indicated. The present discussion will be of the manner in which young birds establish themselves.

After a period of wandering, described elsewhere, the young tend to remain in a limited area which is not necessarily unoccupied and which rarely becomes a permanent territory. Nine individuals trapped in the canyon between August, 1932, and March, 1933, were taken and seen only in certain parts of it. Two, A175116-A and A175117-B, were found in the lower part of territory viii and on the margins of the adjoining territories, xix, xvii, and iii, during August and September and may have been there longer. F36638-C, one of the 1932 brood of pair xii, was found west of territories xi and xiii in the vicinity of traps 46 and 74 from October to December. Three times he was seen with another bird. During the middle of October, H43119-D was in this region. On October 21 an unbanded bird was with him, and during early November, H43131-E. The latter was not banded until November 3 and may have been the individual seen on October 21. From October to the first of March, male H43118-F was taken in traps on the margins of the brush surrounding the partial clearing between x and xii. Female H43127-G was taken once in November and once in December in this same region. From August to December, A175118-H was found on the south slope between the two roads in the region formerly occupied by pair vi and behaved as if he were the owner of this territory. Female H43101-I was seen in the south part of this region from September on. Another bird, male 101303C-J, seems to have stayed in the same region as I most of the time, but was taken near the mouth of the canyon on October 21. H43133-K stayed along the gully below trail A, and male H43121-L along the gully near trail A. A few others that were taken infrequently were less restricted in their movements, or else trapping was not extensive enough to show the area which they frequented most.

All the young do not show this tendency to settle at the same time. Some show restriction in August, others not until November or possibly later. Probably this difference is due in part to the differences in age and, therefore, stage of maturity of young fledged from a first nest and of those fledged from later nests, and in part to the difficulty of finding an unoccupied area or a tolerant neighbor. By December, most of the extensive movements of the young, such as in and out of the canyon, have ceased. Only two new individuals were taken in this and the succeeding months, when trapping had been carried on during the fall.

The areas occupied by the young birds were on the margins or in little-used parts of the territories of established pairs, or in the thick brush tangles along the gully. Their limits were poorly defined. At times the established pairs

were indifferent to the immature birds or showed only a passing interest in them. At other times typical disputes occurred. Whether the reaction of an adult to a given immature bird was always the same is not known, for no observations of successive encounters were obtained.

By March, 1933, all the young birds that had shown preferences for particular parts of the canyon had disappeared from those parts except I and J, which remained and bred. A few of the others became established, but not where their first foothold had been. Male L was with female G in the region of territory iv of 1932 but both were still going beyond the limits they observed a few weeks later. In the second week of March, male F was trapped twice in the south part of territory vi, 1932, and in the latter part of May replaced male J as the mate of female I. Presumably he was wandering in the canyon between these two dates. Female H43130-M, which was trapped once in November, had joined male xii on his territory by January 5, 1933. The female she replaced was last seen on December 8, 1932. The rest, A, B, C, D, E, H, and K, had disappeared entirely.

Previous to the spring of 1933, the history of the immature birds which acquired territories was usually not known, but certain facts of their acquiring territory are important.

Female F36633-N was trapped in territory xx on March 1, 1932. By March 11 she was with male xi on his territory. The female she replaced was killed in a mousetrap on March 5. Female C41575-O was taken on territory x on February 17, 1932. By February 29 she was with male i. Female F36627-P was trapped and seen in company with another young bird near the mouth of the canyon on February 24, 1932. In April she was with male x on his territory. The female she replaced was not taken during February and March, when trapping was carried on in this territory. Male vi was last identified on May 26, 1932, but was probably still present on his territory on May 30. By June 5 his place was occupied by male C41563-Q. The latter was known to be wandering in the canyon during the spring. Unfortunately, my efforts to identify the female with him were not successful.

The manner of taking up a territory was observed in more detail only once. Male C41352-R was first captured in trap 2 on February 3, 1931. On the 9th he was seen near this trap and on the 10th was retaken in it. On the 12th, he and an unmarked bird foraged for more than an hour above this trap in the brush along road B.

On March 17 he was watched for fifty minutes as he preened, rested, and foraged in the brush below trap 2. My notes include the comment, "no evidence of a second bird." A little later, a wren-tit identified with reasonable certainty as R was seen with two others, probably pair xii, in the brush to the north.

From 9:45 to 11:05 on the 19th, R was seen with pair x between traps 2 and 78. While the three were near the intersection of trails A and D a dispute occurred which involved these three and pair xi. After this, R was seen near pair xi as they worked north along trail A.

During February and March, 1931, R appears to have remained on the margins of the small clearing between x and xii. He had no regular companion. For the most part he seemed to be tolerated when he came in contact with adjoining pairs.

He was not identified again until April 20. On this day he was in the small isolated brush patch below trail A and south of the main mass of brush. (Pl. 14b. This patch was burned over in July, 1931, so that the brush was not so dense or continuous when the air photograph was taken as it was in 1931.) Between 7:30 and 9:00 he went from the lower part of this patch to the top, back down to the lower part, and again to the top. Except for a few intervals of about five minutes, he sang on an average of five times a minute throughout the hour and a half—approximately 450 utterances. When he was at the top the second time, his calls were low and of poor carrying quality, but here a second wren-tit was heard and glimpsed for the first time. The two worked down the slope again. I heard no sounds except a single song and a *krrr* answer, but their low *peet* notes would not have reached me. About 9:30 the two were lost in the lower part and could not be relocated. The male and an unbanded companion were seen again at 11:30. During the rest of April and May he was seen frequently, usually with an unbanded companion though on several occasions he seemed to be alone. Except for the time at which it occurred, this probably represents the typical behavior of a young male during the process of territorial settlement.

An earlier attempt had been made to occupy the same brush patch, which I had checked regularly and had hoped would be occupied since its isolation and open brush would simplify observation. On April 13 an unbanded wren-tit was present and sang at the rate of two or three times a minute during the hour I was near. On the following day a pair were seen and heard to exchange *pit-trrr* and *pit-pit* calls. The male sang, but not as continuously as on the previous day. On the next two days no wren-tits were found in this area; on the 18th one song was heard while I was in the field. None was heard during the first half of the morning of the 19th.

The continuous singing on April 13 and April 20 was in marked contrast to the silence on the 12th and 19th. On each of these occasions a male appears to have found the area and proclaimed his presence in it. Each attracted a mate. Why the first to take up the area did not remain is not clear. The area was probably too small to be a good territory, for R and his mate were occasionally seen to make excursions to the main mass of brush, and finally abandoned the patch without breeding although they remained in it until June.

Analysis of the records of the young males shows that one, J, remained and bred in the area where he first settled. Another, L, established himself in an area which was near that of his first preference but occupied by an established pair until about the time he took it over. One, R, took up an area which had apparently been open for months. Two others, F and Q, remained in the canyon as wanderers until openings occurred, which they promptly

filled. Of the four which did not remain on the area of their first preference, one took up a territory in January or February, one in April, one in May, and one in June.

The records for the young females show that one, I, mated with a young male on the area for which both first showed preference. One, G, either joined or settled with a young male. Another joined a young male which had just taken up a territory. Three joined adult males that had been established for a year or more, and a fourth joined a male whose previous status is unknown. Of these, one joined a male in January, one in February, one in January or February, two in March, and one in April.

Although many details of the method by which a wren-tit acquires a territory are still undiscovered, the general procedure can be outlined. After a period of wandering which results in the dispersal of the young from the immediate region of their origin (i.e., at least beyond the limits of the canyon), the immature birds restrict their movements to a limited area. This, figuratively speaking, places the young males on the waiting list for a local territory, the females for a mate among the resident males or the newcomers.

Which individual is to fill a vacancy, and the time of its doing so, must be determined by various external factors, of which its presence near the area is probably the most important.

What part the condition of the immature bird plays is less clear. During the winter of 1932-33 the vacancies, which did not occur until January or later, were promptly filled. Of the ten individuals that acquired a territory or mate in January or later, three males and four females filled a vacancy shortly after it occurred. For some, the time that passed was less than a week; for others it could not have been much longer. Two other females joined males, but nothing is known about how long the place they filled had been open. One individual, male R, was wandering in February and March although the area he finally took over in April was already available.

If vacancies had occurred in October, November, or December, would the immature birds have been ready to fill them? The fact that in September and October male H and male C gave the full song and defended the regions they occupied suggests that these individuals were ready. Actually, as it happened, they did not persist in these areas. The area of H was unquestionably suitable for a territory. In the fall, he gave the full song and his disputes with the neighboring pairs took place over the old boundaries of territory VI, which he maintained. His behavior was that of an established male, and as such he should have persisted as the occupant of this territory unless he met with some mishap. The only other explanation is that his successor, J, forced him out. In all disputes observed, the one in possession has been the victor; and I doubt if this was an exception. The area of male C was not as satisfactory. Only a relatively poor part of it was not already claimed by established pairs, and they may have driven him out.

In contrast to these, male R even in February and March did not seem inclined to take up a territory. The fact that he was tolerated by the estab-

lished birds is as strong evidence of this as the fact that he was not established. If his behavior had been such as to indicate territorial ambition, he would not have been tolerated.

The available evidence for or against the immature female's readiness to join a male earlier than January is slight. Male H from August to December was answered by a female companion in the manner of old females of established pairs. Probably this female would have stayed with him, but because of his disappearance this must remain uncertain. Female I remained in the same area through the fall and winter, but nothing is known of her relation to males during the fall. For the most part the immature birds wander in pairs composed of a male and a female, which demonstrates that there is some sexual response early in the fall. These associations, however, do not appear to be permanent. The female may change from one immature male to another and will leave such a companion to join an established male. Whether she would settle with her temporary mate if a territory were available is a question of much interest which cannot yet be answered.

My tentative conclusion is that because of differences in age and rate of development the immature individuals vary in the time at which the desire for a permanent territory or for a mate reaches the level at which it responds to opportunity. Some of them are ready in the fall; most of them by January or February, rarely or abnormally not until later. Further observation, or better, experimental removal and introduction of birds in a thoroughly known area, would give a more conclusive answer.

Still other questions concerning the way in which the young acquire territory come to mind, but cannot be answered with certainty.

When a young male wren-tit is ready to take up a territory, does he wait indefinitely in the locality (Hamilton Gulch) in which he first settled, or will he, as the urge increases but is not satisfied, leave the locality and go in search of an opening? The two males, Q and F, which stayed in the canyon three months beyond the time when most individuals are on a territory before an opening occurred, suggests that the males wait rather than hunt for a more remote territory; but these individuals may not have been ready earlier, or may have been turned back at the natural boundaries of the chaparral. Of the ten immature birds that stayed in the canyon for any length of time during the fall, five, A, B, male C, male H, and K, were not present in the spring. A or B must have been a male and the other a female; the sex of K is not known. With the exception of H no clue is available with respect to whether these birds died or moved on in search of a territory.

Is the young male forced to wait until an actual vacancy occurs, or may he carve out a territory for himself from an exceptionally large territory such as II, 1933? A few observations made in 1934 indicate that he may gain a territory by taking over part of one already preëmpted (pp. 255, 281).

Does the female wait for a mate in the locality in which she first settled, or does she go in search of one? Females N and O moved at least a quarter of a mile from where they were first found before joining a male. Would they have

moved on out of the canyon if an established male without a mate had not been available within it?

During the breeding season, a widowed female retained her territory and took a new mate, but outside of this period no record of a bereft female's remaining on her territory and taking a young mate occurred. Is such a female driven out by the young male with or without the aid of his companion, or does she leave to join a new mate of her own accord? On one occasion a widowed female joined a neighboring male and her territory was occupied by a young pair, but the sequence in which these changes took place is not known. Another time, three wren-tits, male C41352 and females C41374 and F17814, were found in the region of territory XVIII during January and February, 1932. After February, F17814, which had been in this same region during 1931, was no longer present. Was she a widowed female finally driven out by the new pair?

When first acquired, the territory is apparently without specific limits. These are determined by experience. The only time a male, R, was watched as he took over a territory, he visited and sang in all parts of the area, but this was so small and isolated that no inference can be made with respect to what would take place under more normal conditions. Another pair, XXII, was definitely established on a territory by the first of March, but was trapped 125 feet beyond the limits it came to observe later. As a result of conflicts with the neighboring pairs, it confined its movements to a specific area. Since the established pairs had already come to recognize certain limits through past conflicts and the newly establishing birds tended to move out from a central area until checked, the conflicts came at the same points as in previous years. Hence, the size and shape of a territory tend to remain the same from year to year even when occupied by new individuals.

#### SIZE OF TERRITORY

Variation in size of the territories is at once apparent from the maps in figures 5, 6, and 7. To obtain values that could be compared, the number of acres in each was computed with the aid of a planimeter. These are listed in table 2. The average size was .8 acre. The three smallest, which were held by pairs III, XVI, and XXI, covered slightly more than half an acre. The largest, nearly  $2\frac{3}{4}$  acres, was formed by the fusion of the 1932 territories of pairs I and II in 1933. The two next largest, those of I and XX, were slightly over  $1\frac{1}{2}$  acres in extent or three times the size of the smallest. (See table 2, p. 278.)

The maximum size of  $2\frac{3}{4}$  acres was undoubtedly exceptional. This territory was the only one that I saw invaded during the breeding season without opposition, with hints that a persistent "squatter" might have gained some part of it for himself. I do not believe this pair would have been able to retain the whole if the extensive natural boundaries had not cut down the chances of invasion and the low ebb of the population had not reduced competition in this year (p. 315).

Probably pairs XXI and XVI held about the minimum area which serves as



a territory. They restricted their movements to these small territories during the breeding season, but left them more frequently than other pairs during the winter. The small brush patch in which C41352-R tried to settle in 1931 was evidently inadequate, for, as already indicated, he and his mate were seen to leave it to visit the main brush mass, and abandoned it by June.

Of the various requirements of a wren-tit which might be factors in determining the size of a territory, food is of course the most obvious. Although

TABLE 2  
SIZES OF TERRITORIES IN ACRES

| Territory | 1931  | 1932  | 1933  | Territory | 1931 | 1932  | 1933  |
|-----------|-------|-------|-------|-----------|------|-------|-------|
| I         | ....  | 1.635 | ....  | XIII      | .... | .611  | .852  |
| II        | ....  | .814  | ....  | XIV       | .... | .844  | .888  |
| II-I      | ....  | ....  | 2.712 | XV        | .... | .588  | 1.092 |
| III       | ....  | .578  | .535  | XVI       | .... | .528  | .524  |
| IV        | ....  | 1.356 | ....  | XVI-XIV   | .... | ....  | 1.368 |
| V         | ....  | .606  | .677  | XVII      | .... | .639  | .749  |
| VI        | ....  | 1.547 | ....  | XVIII     | .... | .830  | 1.043 |
| VII       | .753  | .956  | .956  | XIX       | .... | 1.213 | 1.580 |
| VIII      | ....  | 1.175 | .868  | XX        | .... | 1.675 | ....  |
| IX        | 1.126 | ....  | ....  | XXI       | .... | .537  | .549  |
| X         | .606  | .643  | ....  | XXII      | .... | ....  | .796  |
| XI        | .624  | .642  | ....  | XXIII     | .... | ....  | 1.402 |
| XI-X      | ....  | ....  | 1.264 |           |      |       |       |

data that would permit the correlation of the food requirements of the wren-tit, if it is to survive and breed, with the amount of food present in a given patch of chaparral, are far beyond the scope of the present study, certain inferences may be drawn with respect to the rôle of food in determining size of territory.

Because the food is obtained primarily from the shrubs of the chaparral, variations in the type of shrub might be expected to account for varying amounts of food. A comparison of territories in the three divisions of plant cover in the canyon, however, shows that both the extremes and the average size of the territories were uniform in each type. Territories II, III, VIII, XVII, XIX, and XXIII, on the dry, artemisia- and baccharis-covered north slope, varied from 1.580 acres to .535 and averaged .894 acre. Territories VII, IX, X, XI, XII, and XVIII on the poison oak- and baccharis-covered south slope ranged from 1.126 to .606 and averaged .773 acre. Of those along the gully and adjacent south slope, V, VI, XIII, XIV, and XVI, the maximum was 1.547, the minimum .524, and the average .848 acre. Evidently the differences in the composition of the chaparral and the food it supplied were not the controlling factor for size in this canyon.

The density, or penetrability (for it is largely on the basis of penetrability that I judge the density), and the height of the cover in a given type of chaparral might, by governing the total amount of twig surface, govern the wealth

of food, though, admittedly, the change in such a factor as light in dense and sparse brush would also influence the quantity of food. Two sections of the same type of brush with the same density should yield approximately the same food supply; a thinner stand, probably less per unit of area than a dense one. Accurate comparison of differences in density and its effect on the amount of food available, however, is as difficult as comparison of the quantity and kind of food supplied by different types of chaparral, and comparisons can be little more than speculative.

Territory xvi and the part of territory vi between the two roads appear to have brush of similar density, but all of xvi includes only about 22,906 sq. ft., while the part of vi between the roads includes 35,000 sq. ft. and is only slightly more than half the territory. Likewise, xix and xv appear to have brush of the same density but are different in size, 1.213 and .588 acre, respectively, in 1932, and 1.58 and 1.09 in 1933. With respect to these, brush of similar density did not result in territories of equal size. However, in brush of uniform type but of varying density the smaller territories had the denser brush. Territory xx with sparser brush was larger than xix, xix than iii. Here differences in size appear to be correlated with differences in density of brush.

Certain other facts, however, oppose the theory that the food supply plays an important rôle in determining the size of the area. Six pairs occupied territories i, ii, x, xi, xiv, and xvi in 1932. In 1933, as already mentioned, territories i and ii, x and xi, and xiv and xvi were fused. Hence six of the original individuals occupied the same area that had supported twelve the previous year. Admittedly, food supply might vary from year to year, but pairs iii, v, xvii, xviii, and xxi successfully reared broods in 1933 on the same area that they had used in 1932.

Requirements other than food probably would affect the location rather than the size of a territory. Anyway, standing or running water was not a factor, for rain, fog, or dew appeared to supply a sufficient quantity throughout the year. Refuge and roosting places and nesting sites, likewise, do not seem important, because, so far as they can be judged by human senses, suitable places were abundant throughout the chaparral.

These vital essentials being ruled out as determining size of territory, other possibilities were investigated. A comparison of the sizes of territories at the margins and at the center of the brush area showed that those territories which had no other wren-tits on two or more sides averaged 1.276 acres, whereas those which were surrounded on all sides by other wren-tits averaged .651 acre. Territories which were nearly surrounded by others but had a short open boundary of grassland averaged .899 acre. The material on which these averages are based is shown in table 3. The difference of .56 acre between the average sizes and the relatively little overlapping of the two extreme groups suggested that here was a significant factor, and attempts were made to analyze it further.

The possibility that size might be dependent on the number of pairs to be

held at bay occurred to me. The correlation between these, however, as determined by the rank-difference method, was only .28 with a probable error of .107. In view of the principle that length of front favors attack and weakens or overburdens the defense, the total length of frontier to be defended was considered next, as a more accurate measure of the effort a pair would have to exert to maintain its territory. Again the correlation, although positive, was low, .33, with a probable error of .105.

TABLE 3  
SIZE OF TERRITORY CORRELATED WITH CHARACTER OF BOUNDARY

| Territories with one-half or more of boundary formed by margin of brush |               | Territories with about one-fourth of boundary formed by margin of brush |               | Territories surrounded by those of other wren-tits |               |
|-------------------------------------------------------------------------|---------------|-------------------------------------------------------------------------|---------------|----------------------------------------------------|---------------|
| Territory                                                               | Size in acres | Territory                                                               | Size in acres | Territory                                          | Size in acres |
| II-I, 1933.....                                                         | 2.712         | VIII, 1932.....                                                         | 1.175         | XIV, 1933.....                                     | .888          |
| XX, 1932.....                                                           | 1.675         | XV, 1933.....                                                           | 1.092         | XIV, 1932.....                                     | .844          |
| I, 1932.....                                                            | 1.635         | VII, 1932.....                                                          | .956          | XVII, 1933.....                                    | .749          |
| XIX, 1933.....                                                          | 1.580         | VII, 1933.....                                                          | .956          | V, 1933.....                                       | .677          |
| VI, 1932.....                                                           | 1.547         | XIII, 1933.....                                                         | .852          | XVII, 1932.....                                    | .639          |
| XXIII, 1933.....                                                        | 1.402         | VIII, 1933.....                                                         | .868          | V, 1932.....                                       | .606          |
| IV, 1932.....                                                           | 1.356         | XII, 1932.....                                                          | .789          | XV, 1932.....                                      | .588          |
| XI-X, 1933.....                                                         | 1.264         | XII, 1933.....                                                          | .789          | III, 1932.....                                     | .578          |
| XIX, 1932.....                                                          | 1.213         | XIII, 1932.....                                                         | .611          | III, 1933.....                                     | .535          |
| XVIII, 1933.....                                                        | 1.043         |                                                                         |               | XVI, 1932.....                                     | .528          |
| XVIII, 1932.....                                                        | .830          |                                                                         |               | XVI, 1933.....                                     | .524          |
| II, 1932.....                                                           | .814          |                                                                         |               |                                                    |               |
| XXII, 1933.....                                                         | .796          |                                                                         |               |                                                    |               |
| X, 1932.....                                                            | .643          |                                                                         |               |                                                    |               |
| XI, 1932.....                                                           | .642          |                                                                         |               |                                                    |               |
| Average.....                                                            | 1.276         | Average.....                                                            | .899          | Average.....                                       | .651          |

In contrast to this, the correlation between size and the length of the natural boundary line which required no defense was .775, with a probable error of .047. Apparently the limits and configuration of the chaparral play an important rôle in determining size of territory. Territory xxi is completely delimited by natural boundaries, I and II nearly so. The road with its cut banks determined the divisions between II and III, IV and XIX, and XV and XIX. On the south slope of the canyon the brush mass, which is partly separated by the small clearing and which was divided into two easily defended territories of above-average size by pairs IX or XVIII and X in 1931 and 1932, does not readily lend itself to division into three of average size.

It must also be taken into account that the break between many of the adjacent territories, notably that between XVI and its neighbors, occurs where the brush is continuous, and must represent the zone of equilibrium of the pressures exerted by the pairs upon each other, though it must not be thought that established boundaries yield readily to changes in surrounding pressure.

Such boundaries are determined not only by the number of pairs present, but also by the experience of the individuals in previous years.

These two factors may be illustrated by the record of the birds occupying the upper part of the canyon. In 1934 a pair of young birds had crowded pair II-I, 1933, into the area occupied by pair I, 1932. The area occupied by territory XXIII in 1933, possibly with a narrow slice from territory III, was occupied by three pairs. Here were ten birds in an area previously occupied by four. The exact boundaries between the four new pairs were not determined, but two pairs were above road C, with a boundary about where the one between II and VI, 1932, had been, and two were below road C and above road B, the space being divided about equally between them. Even more striking is the fact that little if any change in the original boundaries of VI occurred where it was in contact with long-established pairs in the central part of the canyon, either when territory VI was taken over by pair XXIII or by the three new pairs. The established pairs maintained this boundary although the additional number of birds in the area of XXIII must have increased the amount of pressure.

Can compression by the coming in of additional individuals go on indefinitely? Huxley (1934) found that the territories of coots were compressible, but only to a certain minimum. Pickwell (1931) says that the territories of horned larks were greatly compressed by the growth of vegetation and sometimes abandoned. Should more birds come into an area, I do not think that normally vigorous individuals in possession would ever be forced to vacate. They would, as did pair II-I, give up ground held in excess of a certain minimum, but would defend that minimum with a vigor brooking no defeat.

Does this minimum size depend on an amount of ground which a bird must possess, for reasons deeply hidden in the psychology of the race, in order to acquire a mate and go through with the complex activities of the reproductive cycle, or merely on an irreducible economic quota necessary to feed the pair and their young? The control of reproductive activities by intangible factors somehow connected with territory is illustrated by the absence of casual matings between wandering males and females which are able to subsist at all seasons without territories. There is little doubt, judging from the experience of collectors, that such wandering birds, so far as gross and visible physiological condition is concerned, are ready to mate. Yet, whatever its origin, without territory they do not or cannot mate. The territorial motive in the higher groups of birds is woven more deeply into the psychological skein than economic considerations imply.

I do not mean that territory is not important in supplying food. I believe that the possession of territory is of immediate and practical advantage to the wren-tit, since it limits the number of individuals in a given area and insures a quickly available supply of food when the young are small, but I do not think that the total amount of food available in a given area and the food required by a wren-tit are at all closely balanced. Usually the relation is weighted in the direction of excess food. A better understanding of the relationship and relative importance of the psychological and economic factors

might be obtained by comparing the sizes of territories in the canyon with those in the salal and huckleberry of the windswept Oregon coast, in the arid artemisia or dense oak chaparral of southern California, and in the manzanita and ceanothus of the Sierran foothills.

## REPRODUCTIVE CYCLE

### THE SEASON

In the San Francisco Bay region, nesting activities begin late in March or the first part of April. My earliest date for a complete set of eggs is April 10, 1932. Newberry (1916) found one on April 3, 1915. Several records from southern California, notably one by Sharp (1907) of nestlings on March 11, suggest that the cycle may begin earlier in that latitude.

The length of the cycle in individuals depends on the success of the adults in rearing young. If the first nest is successful, the young leave it sometime near the middle of May. Since they normally remain with the adults for about six weeks, the reproductive cycle would terminate in the latter part of June. If, however, one or more nests are destroyed, the period may be greatly extended. My latest record is a family of young fledged on August 2, 1933. These would not have left the home territory before the middle of September.

### NUMBER OF BROODS

Only one brood is raised. Pairs which successfully fledged young have been watched, but no evidence of repetition of the nesting cycle, once it is completed, has been found. If the eggs or nestlings are lost, in April, May, and at least the first half of June, a new nest is at once begun. I have records of as many as four and five attempts to raise young on the part of one pair, and of the initiation of a new cycle when the brood was lost when about ten days old. Mr. Ernest I. Dyer told me of a pair of wren-tits which he believed had started a second brood soon after the first left the nest. Possibly if the young are lost a short time after they leave the nest, the cycle of the adults is incomplete and begins again; but from my own observations I believe that if any of the young survive, the cycle is not repeated.

### NEST SITE

The situation of the nest within the territory varies; 60 per cent of 47 nests were near the edge rather than the center. Suitable nest sites do not seem to be more common at the margin of a territory than at the center. Some nests, such as those of pairs IV, VI, XX, IIa, VIII in 1932, XXII, IIa, c, and XVIII in 1933, appear to be situated as far as possible from points of frequent contact with other pairs, but this is not obviously true of other nests and cannot be true of some, such as XII in 1932. Certainly the nest is not a center from which the activity of the pair radiates equally in all directions.

Nest sites of the same pair for one season or successive years may be near together or widely separated. The same site was never used twice. Usually the growth of the plant is enough to make a site unsuitable in the following year.

The nest is usually placed at the edge of a continuous mass of brush or where there is a break in it caused by a small clearing or by the lessening height of the bushes. If the brush is scattered, the nest may be in any small bushy plant. Where the brush, whether dense or sparse, is continuous and all of the same height, no nests have been found. This may be because the observer has difficulty in getting through such brush to follow the birds; but the more probable explanation is that only on the margins or in the open does a plant have a growth form which meets the wren-tit's needs.

In *baccharis* the nest is commonly placed in the cluster of new shoots that grow out from a crotch of the larger branches, less frequently in the twigs of the leafy crown; in either place leafy twigs screen the nest from view on all sides. In other shrubs, a comparable location is selected. Typical locations are shown in plate 11.

Within the limits of these requirements, the nest may be anywhere from near the top of the bush to near the ground. Of twenty-five nests that I measured, a height (to rim) of 18 to 24 inches was most frequent, although the range was from 12 to 42 inches. This agrees with the records given in the literature. Rarely, the nest may be at a much greater height. Mailliard (1902) found one in a live oak 12 feet above the ground, Ray (1909) one in an alder at the same height. Dr. A. H. Miller (MS) collected one in a live oak tree 15 feet up; the tree was on a slope with the nest on the downhill side.

In Hamilton Gulch, *Baccharis pilularis* was selected for the nest site in 31 of 44 choices. Other bushes used and the number of times for each are: blackberry tangle, 3; artemisia, 2; hazelnut, 2; poison oak, 1; sticky monkey flower, 1; *baccharis* and artemisia, 2; *baccharis* and brake fern, 1; and *baccharis*, blackberry, and poison oak, 1. In other localities where the birds live in different kinds of chaparral, other shrubs are used.

Support, both under and at the sides of the nest, is found either in a crotch or in a group of twigs built into the outer wall or lashed to the nest. Of thirty-two nests, the support consisted entirely of horizontal twigs fastened to the sides and floor in five, of vertical twigs similarly used in eight, of a combination of horizontal and vertical twigs in eleven, and of a crotch of larger branches in eight. Seven of the thirty-two nests were entirely supported by twigs worked into the sides; one had the support entirely under it. For the majority, the support was fairly rigid and would not sway in a wind. The four or five nests near the tops of bushes were less stable, and one which was built near the end of a horizontal branch of the sticky monkey flower swayed freely.

The support seemed adequate for all but four. Three of these gradually tipped down on the least supported side during the period of use. Young were successfully fledged from one, and the disappearance of young and eggs from the other two seemed in no way related to the condition of the nest. One side of the fourth nest was raised by the rapid growth of the brake fern to which it was attached. The nest was tipped to a perilous angle, but the young remained in it until the normal fledging time.

## NEST MATERIALS

The first description of a wren-tit's nest is that of J. G. Cooper (1870) and his brief account apparently served as the basis for all descriptions of the nest until at least the beginning of the twentieth century. Later descriptions, such as those of Reed (1904) and Pierce (1907), give a more detailed account of the material used, and in two of three nests found by Dr. A. H. Miller (MS) cobwebs are recorded as a constituent.

All the wren-tit nests which I have found were made principally of bark fiber bound together with cobwebs. Bark fibers that I have seen collected and incorporated into nests include old-man sage (*Artemisia californica*), lupine (*Lupinus albifrons*), snowberry (*Symphoricarpos albus*), thimbleberry (*Rubus parviflorus*), nine bark (*Physocarpus capitatus*), baccharis (*Baccharis pilularis*), cow parsnip (*Heracleum lanatum*), and elderberry (*Sambucus glauca*). This material was taken from the dead or old and weathered parts of the stems or branches. Using the bill as a pair of tweezers, the birds grasped a frayed end of bark, or picked at a limb until an end had been loosened, and then, by pulling upward and sidewise to the full stretch of legs, body, and neck, peeled off a narrow strip. In doing this, the bill hold was usually shifted so that the strip was finally held near its center. One strip after another was collected until the bill bristled with them before the load was taken to the nest.

In all nests, cobweb was used to hold the bark strips together, and was a large component of the nest. Egg cases and cocoons were sometimes used, but more often fluffy masses of loose cobweb were brought. The wren-tit's method of obtaining the latter was not discovered.

Much of the material is collected near the nest site. One pair that was watched throughout a day got a great deal of its material from within a radius of ten feet, but at intervals went farther. A nest from which young or eggs have disappeared is usually a source of material for the next nest.

## NEST CONSTRUCTION

The construction of the nest may be divided into four stages: the building of the cobweb framework, of the platform, of the walls of the cup, and of the lining of the cup.

The nest is begun by stretching a cobweb network between the twigs that are to support it. This network at first loops from one twig to the next in a series of single or overlapping festoons. Their fabrication has not been watched, but they must be made while the builder perches on a twig, sticks the mass of cobweb to it, and draws out fibers that are stuck to other twigs. As the work progresses, the ring is crossed by a number of diagonal strands until the network is saucer shaped. Then coarse bark fibers are introduced, sparingly at first, until the platform is from half an inch to an inch and a half thick and about four inches in diameter. As soon as it has enough body, the birds perch or sit on it while working.

After the platform is well advanced, finer bark strips are brought and

placed on the outer rim so that the saucer-like platform is gradually transformed into a deep cup. I have watched the work at this stage closely. The loads of bark strips, two to four inches long, are often dropped on the edge without any effort to arrange them, but after two or more trips (and always, when cobweb is brought) the bird spends from two or three seconds to several minutes arranging the material and building it in. As dropped from the bill, the bark strips are more or less in order and need only to be fastened in place. This is done with the cobweb. The cocoon or mass of threads is stuck to some point of the outer rim. Then a strand is teased out, drawn over the surface of the rim or wall, and stuck to another point, which may be inside and opposite the point of origin or one or two inches diagonally away from it. Often the strands appear to be woven back and forth through the bark strips—an irregular warp and woof with the bill acting as the shuttle. This is repeated until the whole mass has been spread about in a binding network. Ends of bark fiber are tucked in and held with a strand of cobweb. Sometimes strips are moved from one place in the nest to another. At least by the time the walls are started a great deal of time is spent in molding the nest. Occasionally the nest is inspected from near by and some bit of bark adjusted.

When the cup is of the requisite depth, cobwebs are stretched over and woven into the rim until it becomes smooth and firm. Finally, a lining of fine round fibers is inserted. These were often taken from the outer coat of the bulb of the soap plant (*Chlorogalum pomoridianum*), but fine grass stems are also used. The crisscross strands of the lining form a fine mesh and conceal all the bark strips of the wall. The lining is well shown in plate 11. During this stage the nest may be "decorated" externally by the addition of small bits of lichen, but this is not always done.

#### BEHAVIOR DURING NEST BUILDING

The length of time spent in building a nest varies with the number of the nest for the season. If it is the first, parts of seven or eight days may be used; if it is the second or a later one, the time is usually shorter. In June a nest was completed in three days.

The difficulty of finding nests, particularly at the time the birds are building, has made it hard to determine whether more than one nest is started or built at a time. By the majority of pairs, only one appears to be built. After the loss of the third nest, however, pair XIX, in 1932, built and completed a fourth except for the lining, tried out another site but did not complete even a cobweb network, and then completed a fifth nest and laid in it. Pair XIV completed in three days a nest including a lining, and on the fourth day began pulling this nest apart, presumably for use in another nest, though the latter was never found. Pair XI built a nest and on the second day after its completion had pulled material from it. Four pairs—X, 1931, III and XIII, 1932, and XXI, 1933—started nests which they did not complete. Still another pair, IV, 1931, completed a nest but laid no eggs. After nine days some of the lining had been removed. Four days later the nest was relined and finally used. Appar-



ently the birds work on only one nest at a time, but may abandon a more or less completed nest and start over at a new site.

A few times, the cause of the desertion may have been my discovery of the nest; but the species seems less sensitive to such disturbances than many

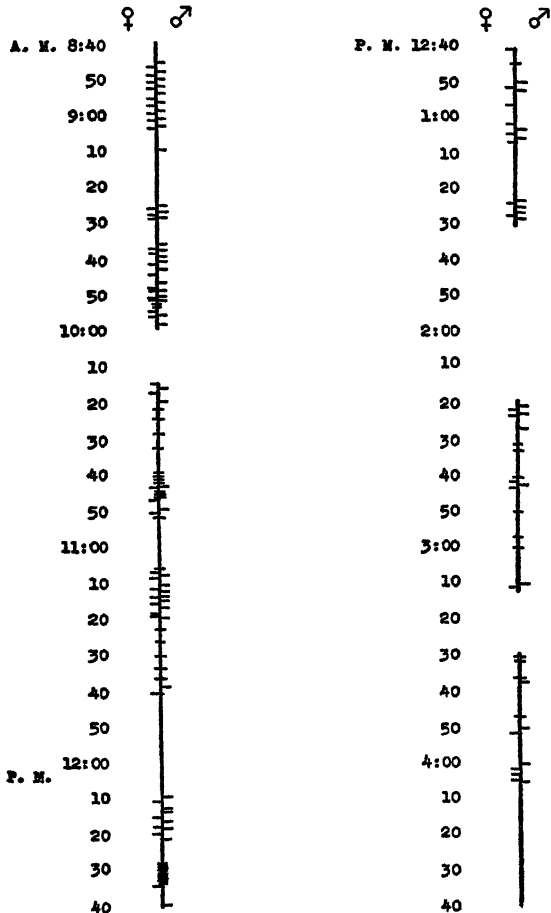


Fig. 12. Visits to a nest during its construction for part of April 18, 1930. † male; † female; † sex unknown; break in vertical line indicates observation of pair away from nest.

others. Two nests found in early stages were completed and used, and those in which an egg had been laid were never abandoned unless the set was destroyed. Two incomplete nests were not found until after they had been abandoned. For these and for most if not all the others some other explanation of the abandonment is needed. Howard's (1929) view that the progress of the reproductive cycle is controlled by the physiological condition of the female is pertinent. In the occurrences of desertion cited, the female probably had not progressed into the fourth or egg-laying phase, and, because the pair remained in the third or nest-building phase, they could respond to the external stimuli only by building and rebuilding to the limit of the stage they had attained.

Both birds take part in all the activities of building. Figure 12 is a graphic record of the activity at one nest on April 18, 1930. This pair was not banded, so that the sex of the bird at the nest could be recognized only occasionally by voice or behavior. Later attempts to watch nest building usually met with such vigorous protest, as well as refusal to build while I was near, that no comparable record was obtained from any of my marked birds. Another type of record of activity is shown in figure 10. It shows the movements of a male and female of a pair during four hours of a day on which they were lining a nest. For the male the record is almost complete, but that of the female is fragmentary. Work goes on throughout the day but is less regular or ceases toward the end of the afternoon. In actual time, as the graphic analysis shows, at least one-half of the working period is spent gathering material or building, but the work is not continuous.

In this period, a variation of the usual *pit-trrr* song is frequently given, and sexual flight and copulation take place. My field notes include the following:

May 8, 1932, 8:50 A.M.—Green [female] on nest *xixc*; as I came up, she left nest, circled below and east; below trap 96, she was joined by Red [male], sexual flight took place, birds chased rapidly through bush, one close behind other, brush too thick to get more than a few glimpses; after a few seconds (10–20), quiet, birds could not be seen (copulation?), shortly Red seen in bush to west. Nest *xixc* was empty, but was fairly completely, if not entirely, lined. [The first egg was laid on May 10.]

June 14, 1933, 6:44 A.M.—From near trap 78, calls of type that have weak unaccented *pit-pit* (only two) preceding loud accented *trrr*. Not all thus, but most. Given for several minutes, then pair seen moving down slope, went into open *baccharis* . . . at intersection of trails A and D; almost immediately went on, giving same idea of chase. Soon a *pit-pit* call, spaced, from near 78. Quiet for about 30 seconds. 6:49, loud *pit-pit* calls from near 78, then, after a pause, a *pit-trrr* . . . 75 feet down slope from intersection of trails A and D, call given repeatedly as wren-tit moved up slope toward this point; female seen here, came from up slope near 78; two chased briefly through brush. [This pair were building a nest, but did not lay in it.]

April 27, 1932, 8:15 A.M.—Saw wren-tit in brush below trail C at bend. It called *pit-pit-trrr*; a second flew down from upper slope, two seen here, worked south around bend, calls *pit-trrr* and *trrr* only from here, then quiet; . . . pair seen here, one . . . [male II] had a few strands of nesting material in bill. Other . . . [female II] no nesting material as near as I could make out. . . 10:29, . . . five songs from male II, second bird near, 4th call was a long drawn out *trrrrr* (bird mounted). [This pair were constructing their second nest for the season. The first egg of this set was laid three days later on April 30.]

Of 15 recordings of the sound that was described as *pit-tr-tr-tr-tr*; *perrrrrt*; musical, repeated *trrrrr*, or weak *pit* followed by long accented *trrrrrrr*, 12 are known to have originated from pairs that were building nests. (For five, the degree of proximity to the time of completion of the nest is not known. The other seven pairs laid eggs 2, 2, 3, 4, 3 or 4, 4 or 5, and 18 days after this call was noted. The pair cited last started one nest, then abandoned it, and built a second.) This call is recorded for the same pair on two successive days and for another pair after an interval of six days. It was twice heard from pairs on the same day that sexual flight was observed. It was twice given when one bird had mounted the other and at two other times when both members of the pair were in the same bush but were not seen. It was not given on two other occa-

sions when copulation was attempted. A few times this call has been heard from pairs in which the phase of the reproductive cycle was not otherwise established, but it has not been recorded at other than the nest-building stage. Copulation possibly followed sexual flight on one occasion, but did not follow sexual flight on two others. It was not immediately preceded by sexual flight on four occasions; the date of one of these was December 8, 1931.

Courtship activities, then, include sexual flight and a distinctive call associated with sexual excitement. Posturing was never observed, but this was probably because of the difficulties of observation rather than absence of such behavior. In sexual flight, the female continually hops or flies away from the male as he approaches, so that a rapid chase through the brush takes place. This chase appears to be the response of the female to the male's approaches before she is ready for copulation.

### Eggs

The length of time that passed between the completion of the nest and the laying of the first egg varied. It was one day for five second or later nests, two days for three nests of which one was a first, one a second or later, and one a third. It was eight days for a first nest. The time interval for pair iv, which was mentioned on page 285, is difficult to interpret. From the time the nest was first completed thirteen days passed before eggs were laid, but only two days after it was relined the second time. With respect to the lapse of eight days, the activity of the pair is not known; some building is probably to be assumed elsewhere, since the birds had not progressed beyond the building phase.

The eggs are a uniform pale greenish blue without markings of any kind, and with a dull surface. They are, as a rule, typically oval, but some have a more blunt point at the small end. The number of eggs in the set varies from three to five, but is usually four. Out of twenty-four completed sets that I found, eighteen or 75 per cent had four eggs, four or 16.67 per cent three, and two or 8.33 per cent five. The average for all is 3.916 eggs per set.

The time of the year in which it is laid and the age of the female apparently affect the size of the set. In April, 3 sets of three eggs and 5 sets of four were found; in May, 1 of three, 10 of four, and 1 of five; in June, 3 of four and 1 of five. The average size of the sets for each month is 3.6, 4, and 4.25, respectively. Females known to be one year old laid 2 sets of three eggs and 3 of four; females probably only one year old, 2 sets of three and 4 of four; females two years old, 5 sets of four; females two or more years old, 2 of four and 2 of five; females three or more years old, 1 of three and 4 of four. The average size of the set for each of these age groups is 3.75, 3.67, 4.00, 4.50, and 3.80, respectively. One female laid successive sets of 3, 3, 3 (lost on day third was laid), and 4 eggs when one year old and sets of ?, 4, and 4 when two years old. A female two or more years old laid successive sets of ?, 4, and 5 eggs, and one three or more years old sets of ?, 4, and 4. These figures suggest that sets laid earlier in the season or by young females are smaller than those laid later in

the season or by older females, but they do not permit any analysis of the rôle of either of these factors.

The eggs are laid at about twenty-four-hour intervals until the set is complete. The times at which two successive sets were laid by female XIX are known. In 1932, the eggs of the second set were laid between 10:30 and 11:30 A.M. on April 27, 28, 29; the eggs of the third between sunrise (5:05) and 6:30 A.M. on May 10, 11, and 12. On two other occasions when the time was checked closely, the eggs were laid between dawn and 6:30. On six others the time was not checked so closely; but the eggs were laid before 7:30 A.M. on five occasions and before 9:15 A.M. on the remaining one. The time of depositing eggs, then, varies somewhat and need not be constant for the successive sets of one individual, but typically it is early in the morning on successive days.

#### INCUBATION

On and even before the day the first egg was laid, adults were seen to sit on the nest for periods of fifteen to twenty minutes. On the day the second egg of a set of three was laid, one or the other of the pair was on the nest much of the time between 7:20 A.M. and 12:00 noon. Two reliefs were seen, but others were missed, so that the length of time each spent on the nest was not determined. On the day the second egg in sets of four was laid, the adults were often found on the nest but no record of the amount of time spent was obtained. With one exception continuous incubation had begun on the day the third of a set of four was laid—adults were always found on the eggs and were seen to relieve each other regularly. No set of five eggs was found until after incubation had started. Probably in sets of three or five incubation likewise begins on the day before the last egg is laid.

I have never observed a lapse of time between egg laying and the beginning of incubation, but a pair watched by Newberry (1916) did not begin brooding until three days after the laying of the third egg of a set of three, although a bird was flushed from the nest on the intervening days.

Most of the sets for which I knew the dates of the eggs were destroyed (p. 311) in the early stages of incubation; but in three sets the eggs hatched on the sixteenth day after continuous incubation began. In two others the length of time appears to be the same, but the data are not beyond question. The set watched by Newberry hatched 15 days after continuous incubation began and 18 days after the set was completed.

At the nest, the behavior of both male and female, which share the task of incubating, is identical. Each time a bird returns, the last foot or two of its approach to the nest is the same, but the two members of a pair may use different routes. As the newly arriving bird settles on the eggs, a wriggling motion is used to arrange the eggs under its body. Occasionally, further adjustment is made by raising the body slightly and using the bill to place the eggs. Once settled, the bird remains quiet until relieved by its mate. The back is flush with or below the rim of the cup, the tail sticks up at a steep angle, and when the bird is in repose the chin and bill rest on the rim with eyes and crown of

the head just showing above it. Rarely, the head is turned to the side and thrust into the feathers of the scapular region, as in roosting. When danger threatens, the eye is always open and the head may be raised. The bird remains motionless until the danger has passed or comes within a few inches of

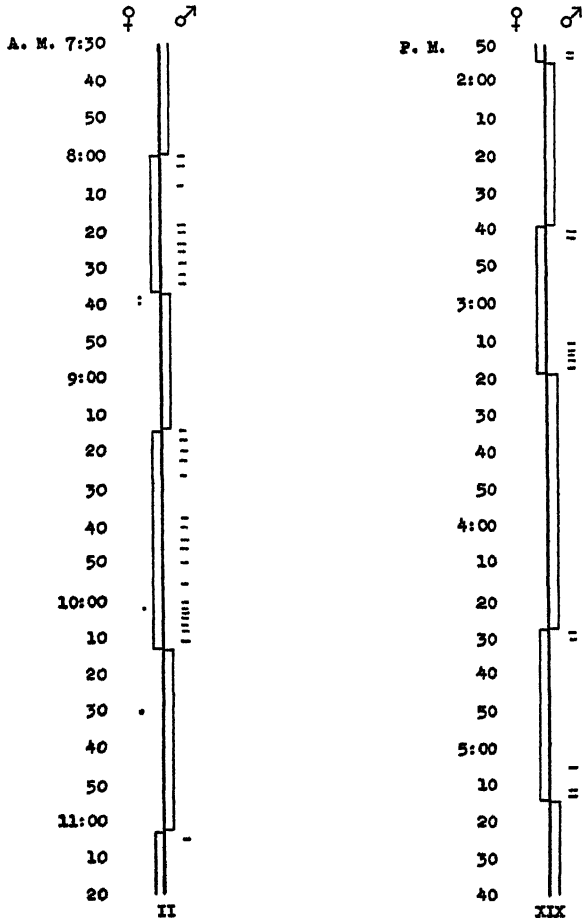


Fig. 13. Records of two pairs for short periods during incubation: pair II on June 19, 1933, pair XIX on April 18, 1932. ] male incubating; [ female incubating; - song by male; . call by female.

the nest. In the latter event, the brooding bird slips off without a sound. It may remain quietly in a near-by bush or it may scold. Sometimes the song or the *pit-pit* call is given.

During the days of the incubation period the activities of the pair follow a set pattern so closely that they can be predicted with accuracy. (A representative record of the activity of a pair is shown in fig. 13. Also see fig. 9.) The female remains on the nest at night. The first indication of activity in the morning is a song by the male from his roosting perch. It is given about twenty minutes before sunrise, when most other species are already moving. The fe-

male responds from the nest with a *pit-pit* call. Both calls may be repeated once or twice. Within ten or fifteen minutes the male comes to the nest bush. As he nears the nest the female leaves, then pauses in a near-by bush to stretch. This includes the simultaneous extension of the foot and wing backward and downward, first on one side, then on the other, fluttering of the wings, flirting of the tail, and turning of the head. In a few seconds she is off in search of food. Fifteen or twenty minutes later she returns toward the nest, and when she is within a few inches of it the male leaves. While still within from three to twenty feet of the nest, he sings, and continues to do so at frequent intervals during the time he is foraging, although less often after he has been away some time. Within thirty minutes, however, the songs increase once more and are uttered nearer and nearer to the nest, the last only ten or twenty feet from it. Then the male goes directly to the nest and relieves the female. As before, she is silent, so that her exact position and behavior is hard to check. Most of her time is evidently spent in foraging; occasionally she scolds a jay or other intruder. In thirty or forty minutes she is back at the nest and replaces the male. As before, his movements are relatively easy to follow because of his frequent songs.

This alternation at the nest, and corresponding periods of quiet and song in the territory, go on throughout the day, but the time each spends away from the nest gradually lengthens so that by nine o'clock the periods of foraging and brooding are forty-five to sixty minutes long. Usually the periods for the male and female are of about the same length, but on one occasion the male's "shift" on the nest was an hour and the female's only half an hour. With the approach of evening the periods shorten somewhat until the last ones are about twenty minutes in length; and finally, when the female returns to the nest, within thirty minutes or less of sunset, no more changes occur. The male sings often as dusk approaches, the last songs coming from near or on the roosting perch, usually the one from which he started the day. The female does not respond and soon complete silence falls, for, with the exception of the Russet-backed Thrush, the wren-tit is apt to be the last bird to sing.

#### HATCHING

Many of the nests found in early stages were not successful, and all the eggs which were marked when laid were lost before hatching. In two nests, two eggs hatched early in the morning, a third later in the day. The fourth egg in one of these nests had hatched by seven o'clock the following morning. One egg in the other nest was infertile. This spacing is what would be expected from the way in which incubation begins. The development of the first two eggs would be started somewhat in advance of the third because the adults sat on the nest during the days these were laid. The fourth egg, which is laid after about twenty-four hours of incubation, hatches correspondingly later. With the exception of the last egg, however, the correspondence in time may be merely chance, for A. H. Miller (1931, p. 173) found that individual variation in development might cause differences of a few hours in the time of hatching.

The young at hatching are without down. The spinal tract shows as a narrow, dark, pigmented area extending from the posterior part of the neck to the middle of the back, where it spreads out laterally; the ventral tract, as rows of light-pigmented spots extending from the anterior part of the breast to the posterior part of the abdomen; the alar, as a dark-pigmented area on the posterior half of the wing; and the humeral, as a longitudinal strip of dark pigment. The crural, femoral, and caudal tracts are not visible. The eye region is large and dark but shows no opening. The skin is light flesh pink in color, the legs and bill straw color. The abdominal wall is so thin that the internal organs such as liver and coils of the intestine show clearly. The young remain in the position of the embryo in the egg, that is, with the legs at the side of the body and the neck flexed so that the head lies along the ventral side. When the nest is jarred, as by the arrival of the adult, the young raise their heads but maintain the position briefly and with difficulty.

The change in the daily cycle of the adults, with the hatching of the young, is surprisingly small. During the first day the adults are more restless and sit higher on the nest than is usual during incubation. The head is occasionally reached under the body to adjust or assist the young. The broken shells disappear, but I do not know whether they are eaten or carried away. Twice, an infertile egg remained in the nest; and one disappeared from a third. Feeding the young begins on this day, but I have not succeeded in fixing the moment of first feeding or the frequency with which food is brought.

#### YOUNG

The activity of two pairs for parts of the day after hatching their young are shown in figure 14. The behavior of the adults is like that on the days of incubation, except that food is brought and the length of each shift at the nest rarely exceeds half an hour and is usually fifteen or twenty minutes. The young are brooded continuously; the bird to be relieved does not quit the nest until its mate is within a few feet. At each relief the adult brings a large mass of food and, while standing on the rim of the nest, distributes it to the young. Each receives its share. After portioning out the food, the adult waits momentarily for the deposition of a fecal sac. If one of the young evacuates, the sac is seized as deposited and eaten by the adult. If none is forthcoming, the adult often pecks the nestling in the region of the anus as if to stimulate defecation. The technique may or may not be successful, but in either event the adult hops into the nest and with a wriggling motion adjusts itself to the contents. Each adult regularly uses its own route (which may be common to both) over the last two feet of the approach to the nest and so always perches on the same part of the rim. When leaving, the bird usually pauses on the rim opposite the point of approach, then flies away in any direction. The male often sings soon after he leaves and continues to sing fairly often while away. He may sing as he nears the nest on his return. On the whole, singing is now much less regular than during incubation and more variation in frequency of song is noticeable among the different males. As a consequence of the rate of alter-

nation of the adults at the nest, the young are fed on an average of three times an hour. The sexes share about equally in the task. Fecal sacs are deposited on an average of one or two in an hour, giving a period of from an hour and a half to two hours for each nestling. The routine may, of course, be altered by

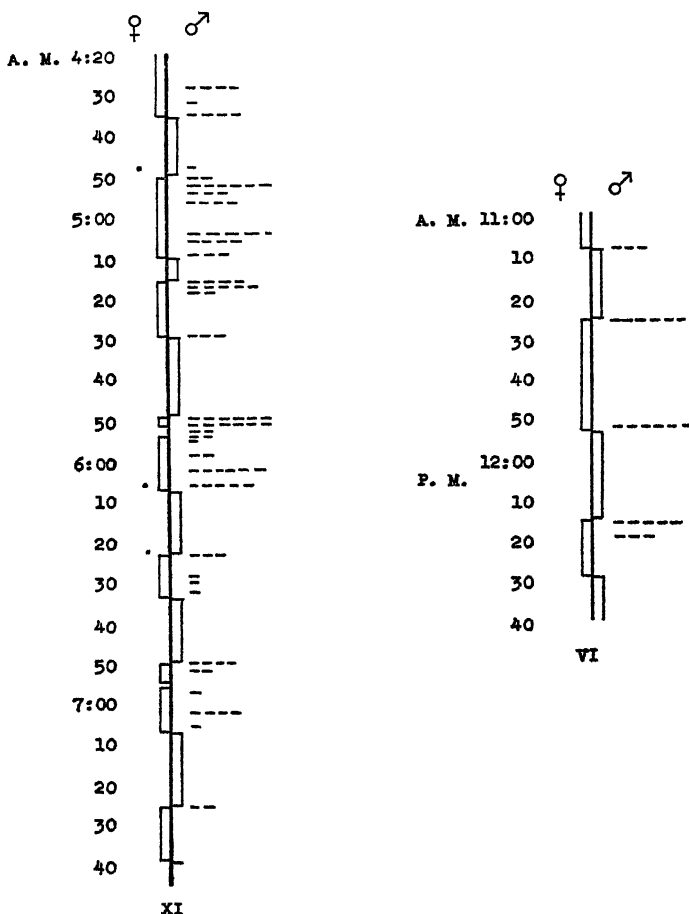


Fig. 14. Records of two pairs for short periods when feeding two-day-old young: pair XI on June 10, 1932, pair VI on May 17, 1932. [ male brooding; [ female brooding; - song by male; . call by female. The adults fed the young on each return to the nest.

the distracting invasion of the territory by other wren-tits or such enemies as the jay. The disputes are brief and ordinarily do not involve the brooding bird, though on one occasion when the encounter was within 20 feet of the nest the female left and advanced toward the center of disturbance.

By the third day the skin of the young in the region of the feather tracts that were visible at the time of hatching shows slight surface irregularities made by the growth of the individual feathers. The feathers of the dorsal side of the head and neck have advanced to nearly the same stage; the femoral tract is now indicated by a dark-pigmented strip and the crural by a few pig-



mented spots. The location of each of the rectrices is marked by a fine hairlike neossoptile a millimeter long. The head is steadier when held up for food; but no other difference in behavior was detected. The behavior of the adults likewise is little changed. Figure 15 gives a record of two pairs at different hours

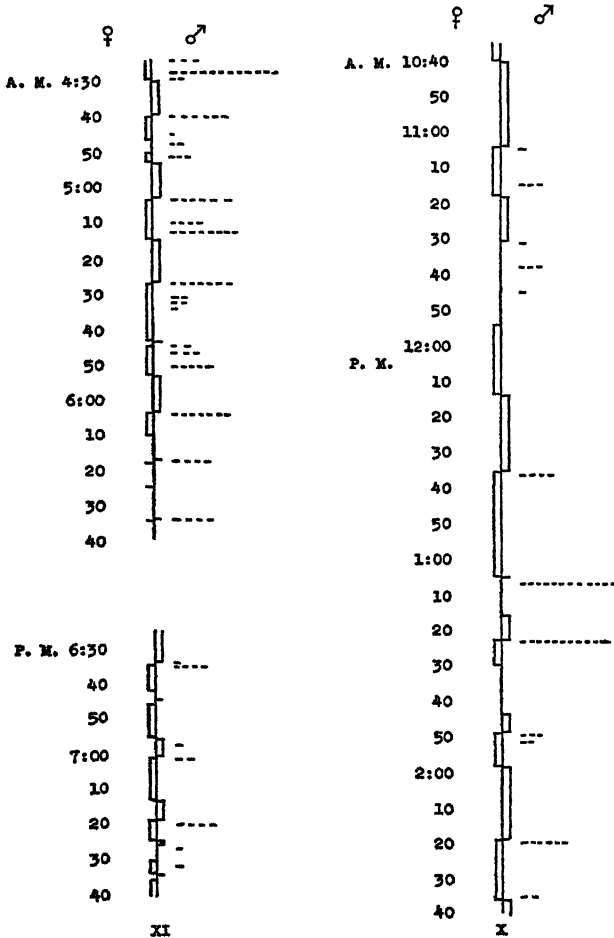


Fig. 15. Records of two pairs for short periods when feeding three-day-old young; pair XI on June 11, 1932, pair X on May 7, 1931. [ male brooding; [ female brooding; - song by male.

during the day. An adult returns to the nest with food on an average of three times an hour and gives a portion of it to each of the young. It then usually remains at the nest and broods, but the young may be left uncovered for 5- to 10-minute periods during the day. Always, the fecal sacs were eaten by the adult. On one occasion, the brooding female "exploded" from the nest and flopped and fluttered away through the brush. The cause of her alarm was not detected. On the fourth day an adult fluttered or tumbled away from the nest as I approached, and was later seen on or near the ground vibrating its wings so rapidly that a whirring sound was produced.

By the time the young are five days old, the feathers of the dorsal tract are indicated by slight ridges with the tips of the feathers protruding above the surface of the skin. A second area of pigmentation shows in the pelvic region of this tract, but in this the individual feathers cannot yet be distinguished. The feathers of the ventral tract are similar to those of the dorsal region. Those of the cervical region are beginning to develop and those in the interramal and malar regions are clearly indicated. The humeral tract is similar to the dorsal. The femoral and crural tracts lag somewhat behind the others. In the alar tract most of the feathers of the dorsal side are indicated by ridges. The flight feathers have grown enough to show as points a millimeter long and these give a scalloped edge to the posterior margin of the wing. The coverts are now plainly distinguishable. The ventral side of the wing shows a few pigment spots on the patagium, but not elsewhere. The vestigial neossoptiles at the tips of the rectrices are three millimeters long, but the feathers proper do not protrude above the skin. The eyelids have separated in a slit about a millimeter and a half long. The apterial skin in general is dark flesh color. The legs and toes have darkened, as well as the bill at the tip and along the culmen. The thickened corners of the mouth are still light straw color.

The resting posture is now upright rather than on the side. The body rests on the belly, the legs along the sides with the toes just touching the nest, and the head usually extended so that neck, chin, and bill rest on the inner wall of the nest.

On the fifth day, the adults spend little time brooding. The sixth day was the last on which any continuous brooding was seen during the daytime. For the few times that sex was determined, the female was the brooding bird. Food is brought on an average of eight or nine times an hour and some of it is given to each of the three or more young.

By the seventh day, most of the body feathers of the young have risen about a millimeter above the surface of the skin but none has broken its sheath. The remiges protrude about three millimeters beyond the edge of the wing and likewise have not ruptured their sheaths. The caudal tract is indicated by pigmentation, but the feathers do not show above the surface of the skin. The skin has darkened still further and the legs are flesh color. The bill has darkened medially, but the sides are yellow-orange. The throat is rather yellowish flesh color. The eye shows a two-millimeter slit, but the eyes are kept closed except when an adult comes to the nest. The body rests on the abdomen and is braced at the sides by the feet, which rest on the nest for the entire tarsal length. In repose, the neck is usually doubled in an "S" curve and the head rests on the side of the nest or on one of the other young. The foot tries to grasp any object it touches, but it is incapable of gripping. The young, as before, respond to the least touch of the nest or twigs supporting it by raising their heads for food.

Although food is still brought to the nest on an average of eight or nine times an hour, the increased capacity of the young results in the feeding of only one or two or rarely three at each visit. Hence, the frequency of feeding any youngster is perhaps not greatly increased although the total bulk of food

given unquestionably is. No rotation in attention to the nestlings was detected, but the first bird to raise its head, if only by a fraction of a second, is served first, rather than any other bird nearer the adult. Invariably, all the young raise their heads at each visit. One receiving no food or a small portion may continue to hold its bill up for several seconds. Often the adult repeatedly thrusts its empty bill into the throat of the young until the latter subsides. This thrusting of the empty bill into the throat of the young was also noted by Newberry (1916). There is probably no regurgitation, for the bill and throat of the adult seem quite empty and the thrusts are rapid in-and-out movements during which the bill is not opened. The fecal sacs are now regularly carried away by the adults.

On the tenth day, the young as seen in the nest give the impression of a nearly complete covering of feathers, but close inspection shows that the feathers are still much too short to cover the wider apteria except when the bird is huddled in the nest. In the dorsal region of the spinal tract the feathers are about ten millimeters long, but six millimeters or more are enclosed in the sheath. In the pelvic region and on the head the feathers are just breaking through the sheaths. The feathers covering the rest of the body are similar in their development. The remiges extend thirteen millimeters beyond the edge of the wing and are free from the sheaths for two or three millimeters. The rectrices extend four millimeters beyond the surface of the skin and have just ruptured their sheaths.

By the twelfth or thirteenth day, the feathers are long enough to cover the apteria and most of them have broken their sheaths. The remiges are nineteen millimeters long and the rectrices seven or eight.

The young are quite active and stand up in the nest, stretch, preen, and flutter their wings. About this time a faint, plaintive food call, *wheat*, is given as the adults approach. The adults do not have any special calls that are given to the young. Food is brought on an average of fourteen times an hour and is given to one or at most two of the young at each visit. The adults share equally in this work. The female still sits on the young at night. Two brief records of observations at the nest are shown in figure 16.

On the fifteenth or sixteenth day after hatching, the young leave the nest. On two occasions of which I have record, they left before 7:30 A.M. on the fifteenth day. The brood which Newberry watched left the nest at 1:30 P.M. on the sixteenth day.

By the day on which the young leave the nest, the plumage covers the body completely, but many of the feathers, the remiges in particular, still have sheaths at the bases and have not yet attained full length. The rectrices are not more than one inch long and are all of the same length so that the tail is square ended. The iris is white. The legs have darkened but are still large and fleshy compared with their condition in the adults. The bill is dark except at the gape, which is now bright orange in color.

I have not been fortunate enough to see the young leave the nest. Newberry states that about 1:30 P.M. all the nestlings fluttered from the nest at the same

moment and remained perched upon near-by branches. It is possible that the presence of the observer may have had to do with this simultaneous departure.

On two occasions of which I have record, one of the young remained somewhat longer than the others. On one of these occasions a single bird jumped out as I came near while hunting for the nest. It fluttered to the ground and down the slope five feet or more into the brush. Simultaneously, one of the

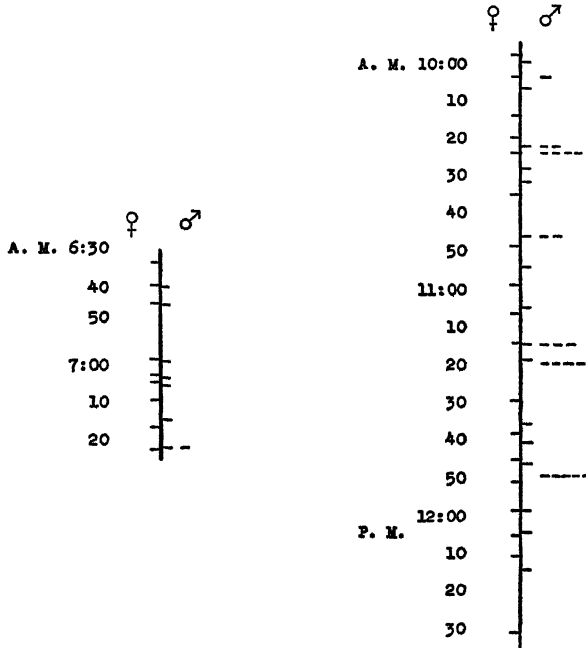


Fig. 16. Records of pair x for short periods when feeding twelve- and thirteen-day-old young on May 16 and 17, 1931. | male feeds; - female feeds; - song by male.

adults made off in the opposite direction. At first its actions suggested the uncontrolled flopping of a decapitated chicken, but later it was seen merely vibrating its wings and hopping from one twig to another. My desire to make out the behavior of the adult made the ruse successful, for when I directed my attention to the young bird it was not to be found.

Another time, three of the young had already left and were about fifteen feet down the slope while one remained in the nest. This one was fed twenty-seven times in an hour, and most of the feedings were within a single half-hour. Both adults took part, but the female came somewhat more often. The other young were fed frequently by both adults.

One family was evidently frightened from the nest when the young were thirteen or fourteen days old; a newspaper had blown in and may have been the cause. Two of the young were found a hundred and twenty-five feet from the nest at a time not more than ten daylight hours after they had been seen in it. They were still within the territory, but were near the opposite margin from the nest. One of the young was missing. The two found were perched side by

side on a horizontal branch about one foot above the ground. They often uttered their faint *wheat* calls as the adults approached. The latter were much disturbed by my nearness and *krrred* vigorously. The young began to move away by hopping a few inches from twig to twig and flapping their wings. All their movements were clumsy.

Two other families have been observed on the day the young left the nest. From 8:30 A.M. until 12:30 P.M. the parents foraged within a small area about fifty feet on a side. Each repeatedly collected billfuls of food, disappeared into a clump of bushes, and reappeared with bill empty. The male sang many times, the female sometimes answering with her usual *pit* call or with a *krrring* sound. At 12:30, as I approached the clump of brush to which they had been going, the young birds hopped away through the brush while the adults circled and scolded me. One of the young was easily caught, but two others, accompanied by the female, made off through the baccharis and all trace of them was lost by the time I had banded and released the single fledgling, which was led off by the male. After ten or fifteen minutes the others were relocated by a *pit-pit* answer of the female to a call from the male. The two young were found side by side near the female, and remained still until my hand was within a few inches of them, when they began to hop from twig to twig, but they were taken (and banded) before they had gone more than a few feet.

Another family was likewise located by the regular visits of the adults to a bush and the frequent *peet* or *wheat* calls of the young. Two of the young were found perched about a foot apart within the leafy crown of a clump of hazelnut bushes. They watched me closely but made no attempt to move when my hand was slowly extended within grasping distance. The lusty *peet* calls of another young bird revealed its position on the ground between two bushes six or seven feet from the first two. When I approached, it fluttered into a bush where it could not be distinguished as long as it did not move, but after a few minutes it called again and moved higher into the bush, where it was captured. All the young were kept in my pocket while a camera was set in position. The adults stayed near, *krrring* and occasionally uttering the usual *pit-trr* or *pit-pit* series. The young, even while in my pocket, responded to these with their low call notes.

When I put one of the young on a twig to photograph it, it made for the nearest bush, but was always easily retaken. When all three were placed on the same twig they remained perched for several minutes. They were clumsy. Often they grasped the twig with only one foot and, when the support of my hand was withdrawn, found their balance by wildly flapping their wings and scrambling for a foothold. If they failed to grasp the twig with both feet, they always slipped backward, and several times would have lost hold altogether if I had not saved them. After the pictures had been taken (pl. 12) and the birds left to themselves, they worked into the hazel bush from which the adults had been calling. On the following day the reaction of the young to the alarm notes of the adults was so perfect that the young could not be located.

One family was observed on the third day after the young left the nest, that

is, when about nineteen days old. The general position, which was within forty feet of the nest, was determined by the calls of the male. As I approached this point, the faint *peep* calls of the young were heard, and the birds were found on the edge of a dense tangle of poison-oak stems not more than two feet above the ground. The four young were perched side by side on a three-eighths-inch horizontal stem, two facing in one direction and two in the other. On my approach, the adults *krred* for a few minutes but soon continued their normal routine. When first seen, the young and an adult which was near were preening. The other adult brought food, and soon both adults were making frequent trips with food. As they approached, the young reached out their heads, quivered their wings, and gave their food call. The adults perched on a branch a few inches in front of the young and fed only one, or rarely two, at each visit. The food was still put into their mouths, but the young reached out eagerly and took an active part in manipulating it. The trips of the adults were frequent and rapid, for food, chiefly insects, was commonly found within ten feet or less. After a half-hour I tried to shift my position, but before I had circled the tangle the young had scattered. Their calls were louder now and helped me to follow them as they worked through the cover. They could hop a foot or more and found their balance on the new perch with comparative ease. Quite suddenly the calls ceased and the birds were invisible. Certainly they were not out of earshot, perhaps not out of sight, but their technique of escape had succeeded.

Another family was watched on the fifth day out of the nest. They were found near a trapped jay which the adults were scolding continuously. After releasing the jay, I overtook the family thirty or forty feet away. It consisted of four members, all of which half-circled me by a series of short hops and flights through the brush. The young moved with as much skill and ease as the older birds—their progress in agility during the first few days is astonishing. No sounds were uttered as they moved rapidly away. Soon the male returned and sang.

On the seventh day after the young of another pair had left the nest, an adult *krred* when I passed near the young. None of the latter could be seen, though I was certain from previous calls that they were near.

When the young of pair xvii, 1933, were twenty-six days old (eleven days out of the nest), the female was seen to approach one of them, and then to fly back into the brush as she became aware of me. The youngster, which fluttered its wings and begged for food, followed, but the two disappeared before anything more could be seen.

Another family was seen when its single surviving young was twelve days out of the nest. The bill of each of the parents was full of green larvae, but they did not feed the young bird, which I finally saw perched on a low branch near the adults. Its bill opened frequently, but the distance was too great to determine whether it was begging for food or *kring* as were the adults.

When the young of pair xix, 1933, were thirty-three days old, or on the eighteenth day after they had left the nest, the family were observed three

hundred feet beyond their territorial boundary. They were first detected by the *peep* calls of the young. The calls stopped as I came near and the family was soon lost. About ten minutes later they were located again at the same point. Two moved away from the same twig, where they evidently had been resting. The adults, at least, went to a large elderberry tree and picked the berries. Sometimes the berries were eaten at once, sometimes they were carried out of sight and may have been given to the young. Possibly the young were plucking and eating the elderberries, but I could not be sure of this. Later, as the family worked toward me, the young begged for food and were fed with insects. Finally they all went down to the elderberry tree again before working up the slope toward their own territory.

A family of young may divide, some following one parent, some the other. Once I surprised pair III, 1933, with their four- or five-weeks-old young. One adult *krred*, the other gave the *pit-pit* call, and the young uttered frequent location notes. The male moved to the west with two young, which begged, fluttered their wings, and *peeped*, until they were hidden in the brush, when they became silent. The female with the remaining immature bird worked away at right angles to the northern limit of the territory, where she turned to parallel the course of the others. Calls were exchanged by the male and female and the two groups presumably rejoined each other.

Pair VII, 1932, was seen when the young were slightly older. The *peep* calls of the young came from the same clump of brush for ten or fifteen minutes and the adults made frequent visits to it. When I attempted to get nearer the young, the whole group moved ahead of me and were finally driven to a point where they had to cross a road. Four crossed at nearly the same time. A fifth and then a sixth worked some distance along the road and finally crossed. The young were evidently being fed, more or less, though they were well able to keep up with the adults and probably were doing some foraging for themselves.

One thirty-seven-day-old family was discovered by the loud *krring* which could be heard on each side of the path which separated its members. At least three young were present and *krred* in the manner of the adults though not as continuously. Two of the young, or possibly a young and an adult, were seen side by side preening each other.

Two young of pair X, 1931, were trapped at this same age. One of them had lost all its tail feathers and the new feathers which were just breaking the sheaths were scarcely three-fourths of an inch long. The other had all the feathers well grown, and the only evidence of its immaturity was the unworn condition of the feathers. Their behavior when trapped was like that of the adults. One gave the *scree* note. While I put colored bands on the first, the adults *krred* near by. After its release they became quiet and stayed out of sight. When the second was released it *krred*. At this, first one and then the other of the adults approached and *krred*, and all three moved off in the direction from which the adults had come. The young seemed well able to fend for themselves but were still objects of concern to the adults.

Young have been seen with the adults on the twenty-eighth and thirty-fifth days after leaving the nest, or when six or seven weeks old. They apparently stay with the adults for several weeks more but go somewhat beyond the usual limits of the home territory.

When about ten weeks old, they sever all connection with the adults and wander freely. One of the young of pair VII, which left the nest on May 19, 1933, was taken in trap 8, 120 feet from the usual territorial boundary, on July 14, 1933. I am not sure whether it returned to the home area or whether it was fully "on its own." One of the 1932 brood of pair V was trapped by Mr. E. L. Sumner, Sr., at the Botanical Gardens in Strawberry Canyon nine weeks after it had left the nest. These gardens are a half-mile away, in an air line, from the territory in which the bird was banded, and an open ridge lies between. This is the only record I have of any of my birds outside of Hamilton Gulch; but the exodus of the young is general, for, of the forty-six banded, only one has been retaken in the canyon after finally leaving the home territory. On the other hand, from June to October, 1932, thirty-seven immature birds were trapped, usually only once, occasionally two or three times, within a week, as they wandered through the canyon. Undoubtedly many more passed through that were not trapped. During these same months immature birds are often heard in the outskirts of the city, where there is shrubbery but not enough for breeding territories.

After the young leave the home territory, two individuals usually travel together. Rarely, loose temporary groups of three to five are seen. These are not family groups, for the members of a brood wander independently of one another. The association of even two individuals may not last more than a few hours or days, but may last a month or more. Two immature birds are often taken in the two compartments of a trap at the same time, or one or more may circle the trap while another is being banded. When released, the birds may give *krring* or *peeping* notes and go off together.

Soon after leaving the home area, the young male begins to use juvenile song. It is unquestionably a wren-tit song and may have the full ringing quality of the adult's, but is often thin, weak, and tremulous. The trill, which terminates it, is usually more prolonged than the adult's and has a warbler-like quality. On August 4, 1933, an immature bird, which had been banded less than two weeks before, was watched while it foraged with its companion near the boundary between pairs XI and XIV. The marked bird gave the juvenile song ten or more times within twenty minutes. This call is the one heard in the fall in the environs of Berkeley and is often answered by a *pit-pit* call. Since this call and response parallel those given by an adult pair, I believe two immature birds wandering together are a male and female.

### VOICE

The best known of all the utterances of a wren-tit is its song, a series of whistle-like notes all on the same pitch and given at decreasing intervals until they run together in a trill. Grinnell (1913) recorded it as *pit-pit-pit-*



*pit-pit-tr-r-r-r-r*. Slight variations occur. A common one is an increase in the number of separate notes before the trill. Another was peculiar to males iv and iii, and may be written as *pit-pit-pit-pit-pit-trr-r-r-r-r-tr*. Male iv used this rendering more than male iii. Both also used the typical form. Other variations of quality, rhythm, or duration occurred, but were never characteristic of an individual.

The song may be given repeatedly from a single perch or as a momentary interruption while a bird is foraging. The singing posture is alert, the head raised, the tail tilted upward. The entire body, especially the throat and tail, vibrates in rhythm with the notes. If the bird is disturbed the series is usually cut short. Rarely it may be completed as the bird hops or flies to a new perch.

The full song is characteristic of the male. Of the many times I have identified the bird giving it, only once was the individual a female, who gave it three or four times while her mate and a neighboring male were fighting. Two other times under similar circumstances the female may have given it, but the identity of the individual was not certain. Except during a fight the bird giving the full song may be assumed to be the male.

Certain situations in which the male uses this song have been described above, in the discussion of the maintenance and acquisition of territory. The song is also used regularly as a call or answer to the mate. This will be illustrated after the call used by the female has been described. A number of times the song was given by a male after he had been flushed from the nest. Mr. Ernest D. Clabaugh (MS) says that a bird he was carrying in his pocket answered the song of another at large. Once I heard it under somewhat abnormal circumstances. On the afternoon of June 6, 1933, I took one of the thirteen- or fourteen-day-old young of pair viii to use as a subject for photography. On the following day it was left with its parents until midafternoon, when it was "borrowed" again. It was returned at 7:05 the next morning, and in a few minutes the male was seen near the youngster. During the next half-hour, the female was not in evidence but the male stayed within about thirty feet of the nest, made frequent visits to it, and sang repeatedly. The songs had a longer, more musical trill than usual and seemed to be a call to the female. At 7:35 she was seen with the male near the youngster and twice answered her mate's songs, which were now of the typical form.

One call is similar to the song in quality, intensity, and pitch, but all the notes of the series are evenly spaced, so that it does not end in a trill. It may be written as *pit-pit-pit-pit-pit-pit-pit*. The number of notes in the series is usually seven or eight, but may be only two, or more than fifteen. The individual notes are sometimes a *peeka*, *pita*, or *peet* rather than *pit*. The intensity is more variable than that of the male's full song, but differences in loudness and carrying power are not peculiar to individuals.

This call is used mainly by the female, but is used by the male at times, so the sex of the bird giving it can never be taken for granted. The use of this call and the song as a call is illustrated in the following extracts from my field notes.

April 12, 1931, 9:30 A.M.—... [wren-tit] called *pit-pit-trrr*... one to north gave *pit-pit-pit* answer and then worked through brush to point from which other called; two then worked south.

July 29, 1932, 11:17 A.M.—Long-continued *pit-pit* call from near [trap] 8, finally a *pit-trrr* answer a short distance to south; *pit-pit* call repeated, finally a *pit-trrr* answer; *pit-pit* continued through answer.

February 26, 1932, 10:15 A.M.—After [I] released C41574 [female xii] and C41367 [male xii] from trap 59, a *peel-peet* call from direction in which C41367 went, a *pita-pita* answer from the direction of C41574; then a *brr* from this last location, then quiet.

March 11, 1932, 11:40 A.M.—... [at end of dispute] male crossed trail C; a *pit-pit-trrr* call by it, and *pit-pit* answer by... [the female] which had crossed trail C earlier.

March 25, 1932.—[Two wren-tits] seen on south side [of draw] working to south; 11:07, four *pit-pit-trrrrs* from this direction. 11:12, six *pit-pit-trrrs*; 11:19, long *pit-pit* and *pit-trrr* answer; then two clear *pit-pit-trrrrs*, then 0 1 0 1 0 1 0 [0, *pit-pit* call; 1, *pit-trrr*], the *pit-pit* call short, only four syllables; both came from bush 25 feet or so south of draw.

The call typical of the male or of the female may be given first. The answer of the other follows, or may be started before the first is completed. If one bird goes to the other after the calls are given, either the male or the female, or the first or last to call, may be the active one. Such calls and answers may be heard at any time of the day and throughout the year, and seem to give the location of one to the other when foraging or when the pair have been separated by trapping or in the course of a dispute. Sometimes the nearness of the two birds to each other, the repetition of the calls, or their combination with the call peculiar to the period of coition, suggests that the situation is not quite the same. On these occasions sexual excitement probably is a factor and finds partial expression in these calls.

I have repeatedly tried to predict whether the *pit-trrr* call of the male will or will not be answered by its mate, that is, whether it is a directive note or a territory song. But even when I have been following a pair my guess has been little better than flipping a coin. Also, I cannot distinguish singing individuals except by their location, though I have never recorded an occasion on which an individual seemed to answer a bird other than its own mate. Possibly, subtle variations occur which I have missed. If, however, we consider the song as an expression of the intrinsic condition of the male, which is reacted to by other males and by females, the differences in reaction of the female probably result from differences in her condition rather than in variations in the utterance of her mate.

Sometimes the response to the loud ringing call of either the male or the female is a faint burring note, *krrrr*. This short note is also given at intervals as a pair forages and seems to keep the two near together as they work through dense brush where visibility is poor. A loud *krrr* is sometimes given before an individual crosses an open space such as the road.

A somewhat louder *krrr*, often repeated three or four times, is an alarm note. It is given as the bird disappears in the brush when it has been startled. It is often given by a trapped bird, or by another bird which is circling the trap. At times, when I am following a pair that is foraging or a pair that I

have disturbed, I am uncertain whether the sound is one of location or of alarm. It may keep the pair in touch as they escape from danger, but it also may be a warning of danger. I have found repeatedly that I am depending on it to follow the birds. Suddenly, when it stops, they are gone. This disappearance suggests a counterpart of a directive color marking on the wing or tail in some species of birds, which vanishes when the bird alights. However, I cannot see much value in the device against the wren-tit's normal enemies.

A loud, continuous *krrr* which may be kept up for minutes on end is a scolding or mobbing note. At intervals it may be interrupted, only to start again with equal vigor. The bill is held slightly open and the whole body vibrates as the sound is produced. The bird is in constant motion, shifting from one perch to another and following or circling the disturbing factor. If a jay is discovered in the territory, the pair follows it and both birds utter this sound continuously until it leaves. The jay seems quite indifferent. The same note was used to mob a sharp-shinned hawk that was perched in an oak. Once a snake appeared to be the cause. The same sound is often given when I am near the nest, but never by the bird on it. If I remain near the nest, the bird stays near me, continually uttering the note. If I try to keep the bird in view, it usually moves away from the nest and the *krrr* lessens in intensity. I have used this change in intensity to establish the location of a nest, with some success. Similar behavior might result in drawing the wren-tit's normal enemies away from the nest site.

A squealing note, *scree* or *schree*, was heard a few times. Once, it was given by a bird which had its foot caught in the door of a trap, as I slipped its toe out from between the two wires that held it. Three or four times, this note has been given when I reached into a trap to catch the bird, or when I was banding it. The same sound was heard during fights between individuals kept in captivity, once by one of two birds fighting bill to bill, once by male C89928 when another male, C89930, evidently wished to attack it but was prevented by the wire between the two, and on a later day, when both were in the same cage, by male C89928 whenever C89930 darted at him in the course of their frequent disputes. This note appears to be one of fear, defeat, or submission.

The notes uttered in fighting and the one peculiar to the period of coition have been described elsewhere (pp. 270 and 287).

A complex of soft musical *pit*, *puit*, or *puwet* calls and harsher *tuck*, *chit*, or *dot-dit* notes remain to be considered. These calls were heard from four caged birds, two males and two females, when the fourth, a female, was first placed in the same room with the other three. They accompanied the advances and retreats of the two males and the new female (the interest of the old female was mainly hostile) and were mixed with the typical dispute calls as the birds chased through the brush. The movement was usually rapid and the birds so near together that it was impossible to determine whether any of the sounds were peculiar to one sex. Similar calls have occasionally been heard from birds in the canyon when two or more were together. Those of the caged

birds seemed to be part of the process of the recognition of sex, and, as given by the birds actually observed, were the preliminaries of pairing.

The first sound given by the young is a soft *wheat* or *tu-wheat* when they are about twelve days old. It is given as the adults approach with food. A fourteen-day-old nestling that was taken from its parent refused food after swallowing several bites in rapid succession and gave a soft musical trill that suggested contentment.

As soon as the young are fledged, they use a *peet* or *peep* location note which is given when the adults approach with food, as a response to the *pit-trrrr*, *pit-pit*, or *krrr* calls of the adults, or spontaneously. They also use a more vigorous version of the *wheat* call when begging for food. A few times, I have heard the note of contentment mentioned above. The development of the calls typical of the adult have already been considered in the account of the young.

### FOOD

The wren-tit lives primarily on insects, spiders, and small fruits. Things which I have seen eaten are elderberries, snowberries, thimbleberries, poison-oak berries, and many insects too small to be recognized at a distance. A summary of the kinds and quantity of each type of food, based on 165 stomach examinations, has been published by Beal (1907). I successfully kept wren-tits in captivity on a diet consisting of mixtures for soft-billed birds: banana, cottage cheese, lettuce, bread crumbs, and occasional live insects and wild berries.

The wren-tit's forage beat includes the bark surface of twigs, to a less degree the surface of the leaves, and fruiting stems. Rarely, they forage on the ground. Usually, the food sighted by the bird is within "peck range," but sometimes it is detected at a distance of one or two feet and the bird flies or hops to obtain it. Not infrequently an individual flies up and hangs inverted while hunting among the leaves of live oaks for larvae. A few times, individuals have been seen hovering at sticky monkey flowers. One was seen to catch a small butterfly which flew near. The caged birds sometimes tweaked over leaves, thrush-fashion, when provided with leaf mold.

Small objects, such as most of the insects and the poison-oak berries, are swallowed whole; large ones are broken up. After obtaining a large morsel, the wren-tit resorts to a twig, places the object under one foot, and pulls off small pieces with its bill. Snowberries and thimbleberries are regularly handled in this way, elderberries sometimes. The berry is pecked until the skin is broken, and then pieces are pulled off and swallowed. Seeds met with are discarded, though the large flesh-coated seed of poison oak is swallowed and later disgorged. The edges of lettuce leaves which were given to caged birds were held by the foot and pieces from an eighth to a quarter of an inch square torn off. If a larger strip came off, it was placed under the foot and pulled into smaller pieces. Large bread crumbs were held with the foot, or small pieces were broken off with a quick shake of the head.

The attack on larger prey, such as centipedes two or three inches long, as seen in caged birds, is a prolonged process which combines dexterity and speed. The lashing centipede, to a wren-tit, is formidable and inspires obvious fear. It is circled and watched at length, and often succeeds in disappearing into the leaves. Otherwise, the bird finally recognizes an opening, there is a quick thrust, grab, and toss, the centipede lands several inches away, and the tactics are resumed. With each attack the vigor of the prey is reduced. Finally the wren-tit dares hold it with foot or bill, and the bill is worked systematically along the body, crushing as it goes. Sometimes the body is

TABLE 4  
SUMMARY OF CAPTURES SHOWING SEASONAL VARIATIONS

|                                               | April | May | June | July | August | September | October | November | December | January | February | March |
|-----------------------------------------------|-------|-----|------|------|--------|-----------|---------|----------|----------|---------|----------|-------|
| Total number of wren-tit captures             |       |     | 40   | 25   | 21     | 25        | 30      | 39       | 43       | 183     | 194      | 108   |
| Number of trapping hours                      |       |     | 61   | 40   | 32 5   | 40        | 21 5    | 25       | 11       | 54      | 121      | 115   |
| Number of wren-tit captures per trapping hour |       |     | 66   | 62   | 65     | 62 1      | 39 1    | 56 3     | 91 3     | 39 1    | 63       | 94    |

pulled through the foot, whether by accident or design. Finally, pieces are pulled off and swallowed. Once, a captive wren-tit pulled to pieces and ate in the course of half an hour a very active four-inch angleworm, an operation which was not repeated though the opportunity was often provided. It was accomplished with extreme awkwardness, both because of the obvious fear of the bird for the twisting worm and because when a grip was secured the slimy length pulled through the grasping foot. The first wounds were inflicted with the bill while the slippery body was held in both feet. Food of this size probably is not a common part of the diet, though Beal (*loc. cit.*) found parts of grasshoppers and crickets in a few stomachs. Food is usually carried in the bill. Dr. A. H. Miller and Mr. T. T. McCabe told me of seeing one of the captive birds in flight carrying food grasped in one foot instead of in its bill, but this is exceptional.

During most of the year food seems abundant. From the middle of the breeding season (about mid-April) on, large billfuls of insects are found by the adult wren-tits within a short distance of the nest or young, with a few minutes' search. In late summer and fall, insects are still plentiful and numerous berries are available; yet the supply is not unlimited or permanent. Other species of birds in the canyon depend on the berries, and the crop is gradually depleted until, at the end of November, most of the berries are gone. From this time until February and March, although food is still available it is less

abundant. Probably the decrease in natural food is crudely measured by the wren-tit's increasing interest in trap bait as represented by the increasing rate of captures (table 4). This rate reaches its highest point in December and January, when it is six times as great as in the late summer, and then decreases. The latter drop undoubtedly is influenced by the bird's increasing preference for insect food and its greater abundance.

The wren-tit makes use of standing water for drinking and bathing when it is available, but during the many months when the canyon is baked and dry it depends rather on the drops of moisture that collect on the leaves from rain or fog. I have often seen these taken by a touch of the bill. Even this is not a daily necessity, for periods of a week or two occur when no moisture is available.

### ROOSTING

The roosting habits of wren-tits were first studied in caged birds, and the findings from this source were checked against the behavior of birds in the field. The individuals of a pair roost side by side, facing in the same direction and so near together that they appear as a single ball of feathers from which tails, wings, and feet protrude—an appearance that is not accidental or occasional, but is produced by fluffing, spreading, and interlacing the body feathers to such a degree that when the heads are turned to the outside and buried, a single ball remains without so much as a line of separation. This arrangement of the feathers is an active process involving both movements of the feathers by the muscles that control them and manipulation of them with the bill. Usually the birds sit so low that the body feathers touch the perch and partly conceal the toes, but sometimes the bodies are well above the perch and then one can see that the inner leg of each bird is drawn into the feather mass, and the weight supported on the outside leg. The angle of the outside leg to the body suggests that the two birds are braced against each other. (See pl. 13.)

If more than two birds were in a cage, their relationship and the length of time they had been together affected the number that roosted on the same perch. When a male was first put into a cage containing a pair, it went to roost alone, but after a week or more regularly slept with the pair. When a fourth, a female, was added, she slept alone for a time. Later, the two birds added slept together at the opposite end of the cage from the original pair. At another time, when five birds were put into a cage, they slept in a row. Whatever the usual arrangement might be, if the birds were disturbed after going to roost, all, whether two, four, or five, roosted together when they settled down again.

Three times I found a pair roosting in the wild in Hamilton Gulch. Each time, the two birds were sleeping together as described above. I was not successful in finding the exact roosting place of a family, but presumably the adults and fledglings sleep together, for at roosting time they keep in close touch and disappear and reappear at the same place.

The caged birds roosted on a horizontal perch several feet above the bushes with which the cage was furnished. When this perch was removed they slept on horizontal branches within the crown of a bush, and marked preference was shown for particular branches, which were used night after night. A bush in which one of the pairs in Hamilton Gulch roosted is shown in plate 14. The pair was found here three out of five successive nights I visited the place.

As dusk falls, a pair works toward the roosting place. The male sings repeatedly until in or near the roosting bush. When the perch has been occupied, some jostling takes place before the birds finally settle. One may jump over the other, or leave the perch only to return and sidle up to its mate. After a few minutes, they remain in place and each quietly adjusts its own or its mate's plumage, or remains motionless with the head drawn in close to the body. Finally, the heads are turned back and outward and placed under the feathers of the scapular region.

Both birds awaken about the same time; or the first to move awakens its mate. They sit quietly for a minute or two, blinking sleepily. Soon they hop away, stretch, and begin to hunt for food. The male sings repeatedly from in or near the bush. Deshler (MS) found that the average time of the last song of the day was twenty-one minutes after sunset, and of the first morning song one minute after sunrise.

### PREENING

A wren-tit's care of its plumage includes the preening and bathing typical of passeriform birds, but a few aspects are of special interest.

Preening is usually done by the individual's working over the feathers with its bill, or, where the bill cannot reach, with its foot. Not infrequently, however, the members of a pair or family preen one another. The activity is usually limited to the region of the head, but sometimes includes the feathers of the back, sides, breast, and crissum. The method is always the same: the bill is thrust into the feathers and a single one is manipulated between the mandibles from the calamus to the tip of the vane. Preening was observed less often in birds out-of-doors than in caged ones, but wild birds were seen to fluff out or work over the feathers momentarily, and a few times to spend ten or fifteen minutes going over the entire plumage. Preening was regularly done after bathing, and was common during the molt period.

The rain puddles that formed in the ruts or depressions along the road were used as baths by the wren-tits which lived near them. Their bathing included the usual bobbing and splashing, but, unlike the other birds I have seen bathing, the wren-tit moistened its plumage by a series of momentary dips rather than by a single long one. Puddles were rarely available for most of the wren-tits in the canyon and were not present at all during many months of the year, so that most of the birds depended on the fog or rain-moistened shrubbery. The operation is unmistakable. The birds move about in the leafy crowns, brushing and bumping against the wet leaves until their plumage

is well dampened, and then the customary shaking and preening takes place. Fog or rain moisture is frequently available, but may be lacking for a week or two at a time.

In the cages, water was always available and bathing was a frequent though not daily occurrence. If one bird bathed, the others showed much interest and often followed suit. In order to observe bathing in moistened brush more closely, I sprinkled part of the brush in the aviary each morning during a period of a week. The first morning, the birds were greatly excited and immediately drank and bathed. On succeeding days, they came to the moistened brush but did not bathe.

Dust bathing was seen only once. This occurred in Hamilton Gulch shortly before sunset. A pair was on the road just at the edge of the brush. One member of it squatted in the dust, shoved forward, sliding along on its breast for about eight inches, and then dipped its head into the dust, at the same time stirring it up with the wings or feet. This was repeated several times until the bird was almost dust colored and much lighter and grayer than its mate. The latter hopped about within a few feet but did not bathe. The dust in which the bathing was done was an inch or more deep and showed a number of channels with slight enlargements at one end where the bird had first pushed its body along and then stirred up the dust.

## AGE

The average length of life of a wren-tit which survives to its first breeding season could, of course, be determined by continuing the population study over a longer period of years, but an estimate can be made from a shorter period. Burkitt (1926), assuming a fairly constant census, which is in accordance with logic and known facts, has derived an equation by which  $n$ , the average age attained by birds that survive to their first breeding season, can

be worked out. This equation is  $my = \frac{1}{n} (2m + mr)$ , or, solving for  $n$ ,  $n = \frac{2+r}{y}$

when  $m$  equals the number of pairs,  $y$  the number of young to each pair surviving to the next breeding season, and  $r$  the proportion of mateless birds to the number of pairs. When the values for  $r$  and  $y$ , which I obtained from field work, are substituted,  $n = \frac{2 + .275}{.513}$ , or 4.43 years.

This value can be checked by determining the fraction of individuals in each age group. In 1933, 10 of the 39 wren-tits present, or 26 per cent, were one year old, 4 to 6 individuals, or 13 per cent, were two years old, and 23 to 25, or 61 per cent, three years old or older. Excluding the unmated birds which did not become established, 15 per cent of the individuals were in the one-year-old group. Using 14 per cent as an average number of individuals in an age group, the 61 per cent of birds three years old or older represent individuals of about four age groups, of which the youngest is three years old, the oldest six or seven years. In other words, about one-fifth of the in-



dividuals are replaced each year. With a constant population this means that the average individual that has survived for one year would live about five years. Such an age is well within the range of possibility. An individual at least ten years old has already been mentioned (p. 267). Another individual was seven years old when last seen, and a third was accidentally killed when five or more years old.

### POPULATION

The geometric rate at which a population of animals is potentially able to increase, and usual failure of a population to increase at that rate, is common knowledge; but little is known of the actual numbers of individuals produced and destroyed in any species living under natural conditions. The technique employed in this study permits the determination of the numbers involved.

The average breeding population of the 16.7 acres of brush in Hamilton Gulch at the beginning of March was 18.5 pairs. In addition, an average of five unmated birds was present. Since the species has an average set of 3.916 eggs and raises only one brood annually, the potential increase for a year was about 72 individuals or 200 per cent. The actual increase was about half this expectancy, for an average of only 33.5 young was reared during a single breeding season. The discrepancy resulted mainly from the destruction of nests, for only 56 per cent of the pairs were successful in fledging broods, and the successful broods averaged 3.35 individuals, or only 10 per cent less than the theoretical value. As a result, at the end of the breeding season the population, instead of being tripled, had been doubled.

From this time on, the number of individuals gradually decreased. In the course of the breeding season, 2 or 3 of the adults died, and during the winter following, 12 or 13; or 36 per cent in the course of the year. The mortality rate of the young birds reared in the canyon was indeterminable, because they became widely dispersed; but since both general probability and my trapping records suggest that a comparable number of immature birds entered the canyon, an estimate of the number of survivors can be made from the number of one-year-old birds that were present in the spring. This averaged 9.5, so that approximately 24 individuals, or 72 per cent, of the young fledged, died in the course of their first winter. On this basis, the total number of deaths equaled 39, or 52 per cent, of the maximum population of 75. Such a death rate would, of course, result in the gradual decrease of a population, and a decrease actually took place during the last year covered by the field work. If the work had extended over a longer period this would no doubt have been compensated for by a period of increase.

By the beginning of the next breeding season, the maximum population had again been reduced to about the level of the previous year, or eighteen to twenty pairs and four or five unmated birds. Whether the slight variations in the minimum size of the population were the result of chance fluctuations or of a small sampling of a population that remains at a nearly uniform

density, as described by J. A. Nicholson (1933) for a territory-holding species, or whether they were part of a cycle of growth in numbers which is periodically cut short, as described by Severtzoff (1934), could only be determined after a longer period of observation.

TABLE 5  
VITAL STATISTICS  
(Symbols refer to the Burkitt formula, p. 309.)

|                                                                                                        | 1931* | 1932 | 1933 | Average |
|--------------------------------------------------------------------------------------------------------|-------|------|------|---------|
| Number of pairs ( $=m$ ).....                                                                          | 18    | 20   | 17   | 18.5    |
| Number of established birds ( $=2m$ ).....                                                             | 36    | 40   | 34   | 37.0    |
| Number of unmated birds ( $=mr$ ).....                                                                 | ..    | 5    | 5    | 5.0     |
| Total population at the beginning of March<br>( $=2m+mr$ ).....                                        | ..    | 45   | 39   | 42.0    |
| Number of young raised during breeding season ..                                                       | ..    | 31   | 36   | 33.5    |
| Total population at end of breeding season.....                                                        | ..    | 76   | 75   | 75.5    |
| Number of one-year-old birds ( $=$ number of young<br>surviving) at the beginning of March ( $=my$ ).. | ..    | 9    | 10   | 9.5     |
| Percentage of young surviving.....                                                                     | ..    | 32   | ..   | 28      |
| Number of birds one year or older dying in the<br>course of the breeding season.....                   | ..    | 2    | 3    | 2.5     |
| Number of birds one year or older dying in the<br>course of the winter.....                            | 8?    | 10   | ..   | 9.0     |
| Number of unmated birds dying.....                                                                     | ..    | 3    | 4    | 3.5     |
| Total number of birds one year or older dying..                                                        | ..    | 15   | ..   | 15.0    |
| Percentage of birds one year or older dying....                                                        | ..    | 30   | ..   | 36      |
| Proportion of mateless birds to number of<br>pairs ( $=r$ ).....                                       | ..    | .25  | .3   | .275    |
| Number of young to each pair surviving to the<br>next breeding season ( $=y$ ) .....                   | ..    | .45  | .588 | .513    |

\* Census not complete this year.

The factors which nullify complete realization upon the potential geometric rate of increase remain unknown, for the most part, but since they must be the agencies of natural selection it is worth while to analyze, as far as possible, what they are and when they are effective.

The decrease that occurred before the young were fledged amounted to about half the total number of individuals destroyed. This loss was about evenly divided between eggs and nestlings. Of 91 eggs, 5, or 5.5 per cent, were infertile, and 23, or 25.3 per cent, were destroyed. The remaining 63 eggs hatched. Of the 63 nestlings, 35 were fledged and 28, or 44.4 per cent, destroyed. With the exception of the few infertile eggs, these losses were the result of the complete failure of a nesting. Of 24 nests which were found before or soon after the set was completed, 7 were destroyed soon after the eggs were laid and 7 before the nestlings were ten days old. From only 10, or about 42 per cent, were young fledged.

Little is known of what caused these failures. None of the nests was destroyed as a result of unfavorable weather conditions. Once, I saw a California Jay take the nestlings; and I have other records of this outside the canyon.

On all other occasions the eggs or young simply disappeared. No doubt jays took some, if not most, of them. Cats, skunks, weasels, raccoons, opossums, and snakes, which are present, may have taken a few. There was no evidence that any eggs or nestlings were removed by human beings. No deaths resulted from failure of the parents to brood the eggs or care for the young. None resulted from failure to build a nest that would stand the wear and tear of rearing a brood, though the final state of some of the nests suggested that this might rarely occur. The importance of the location and concealment of the nest is hard to estimate. Many that seemed well screened were robbed, and others that I thought poorly situated were successful. On the whole, chance, the abundance of the jays, the success of adult wren-tits in hatching broods, and hence greater food requirements, are probably more important than the site of the nest.

Since the young are almost helpless when they leave the nest, this might be expected to be the time of greatest peril. Actually, observed losses were few. Of six broods, all the young survived. Of one, only two of three young were seen after they left the nest; but this brood left a day or two earlier than normal, perhaps frightened out by a newspaper flying before the wind. Two other broods were each reduced to a single young bird soon after they left the nest. Each occurrence may have been slightly abnormal, for I banded the young when they were about fourteen days old, an age when it is hard to handle the nestlings without their "exploding" from the nest. They remained quiet while I was near, but may have left early because of the disturbance. Few losses seem to occur while the young remain on the home territory.

Causes and times of death of young birds after they are independent are almost impossible to determine. The temporary wandering habit makes it impossible either to follow the fates of individuals or to count disappearance as death, yet a clue to the time at which their numbers decrease is given by the number of immature birds trapped during the fall and winter months.

In the lower half of the canyon during the winter of 1932-33, 10 immature birds were trapped in September, 13 in October, 12 in November, 5 in December, 3 in January, and 6 in March. The amount of time spent trapping and the readiness of the wren-tits to enter the traps would, of course, influence the numbers taken. In order to allow for these factors, the average number of wren-tit captures per trapping hour was determined. These values, given in table 4, page 306, indicate that the chances of catching a wren-tit in December are six times as great as they are in September, and about two and one-half times as great as in October and November. These probabilities more than offset the additional number of hours of trapping in September, and about balance the additional trapping hours in October and November, so that the figures for the different months are approximately comparable, or else slightly favor the presence of additional individuals in September. The 50 per cent decrease in the number of immature birds occurred between November 3 to 7 and December 8 to 12, which dates include the trapping days in each month. There was no return to the numbers of the previous months.

This period is also the one in which the adults disappear. (Fig. 8.) Of those pairs which were kept under continuous observation during the fall and winter, five adult individuals disappeared between December 8 and January 5, and two in January. The records for these two months include half of the known disappearances among the adults, and at least two of the other individuals probably died within the same period.

The months of greatest mortality are November and December for the immature birds and December and January for the adults. What is the cause of this sudden increase in mortality? Natural enemies probably do not take a heavier toll at this time. Weather conditions are less favorable, but in the San Francisco Bay region are not severe. Food is less available. By the end of November the berry crop—elderberries, snowberries, poison-oak berries, and others—has been harvested by the berry-eating inhabitants of the canyon. Many insects are less plentiful. The wren-tit's increased interest in the trapping bait is shown by the highest rate of capture, and probably correlates with food shortage. Presumably, the decrease in food, possibly coupled with cold, rain, and wind, results in conditions below a subsistence level for a certain proportion of individuals.

Does the month's difference in time of highest mortality for immature birds and for adults result from previous weeding out of the less sturdy among the adult generations, or from the more or less exclusive possession of a feeding area by the adults? Probably each of these influences plays a part in the apparent greater mass resistance among the weak or marginal adults.

Do the immature birds that settle on a particular area have a better chance of surviving than those that wander? Five of the ten that settled in the fall survived, but no comparable figures are available for the wanderers. After March, four-fifths of the immature birds without territories disappeared, and only one-fifth of those with territories did. Perhaps the former left the canyon, but at least two did not, and new wren-tits, which would be expected if individuals were wandering, were not taken in the parts of the canyon that had been trapped continuously.

After the first year of life how much does the age of an individual affect its chance of surviving? One male and two females died in their second year, one female in her third year, one male and one female when two or more years old, three males and two females when three or more years old, and one female was accidentally killed when five or more years old. The group three or more years old probably represents at least three age groups. These records, though admittedly meager, do not show a differential death rate for individuals in different age groups. If a bird survives its first year and secures a territory, it is as likely to survive as any other similarly situated individual of equal or greater age, short of senescence.

After the first year, what selection takes place is not based so much on the individual's ability to live as on its ability to leave offspring. Of nine pairs that were composed of the same individuals in 1932 and 1933, three had successful broods both years, five fledged broods in one year only, and one failed to fledge

any young. Records for a longer period are needed, and no analysis of the factors that make for successful nesting has been attempted, but the end result must be that the reproductive cycle is adjusted to external conditions and that certain family lines have a greater chance of persisting than others.

On the whole, this analysis of the population does not enable us to go much beyond familiar generalities; yet it shows that a population study of a wild species can be carried on and might, with more workers, on a larger area, reveal many of the laws which control wild populations. Trapping or observation of distinctively banded individuals makes possible accurate and complete census records. The time and extent of the annual increase and decrease in numbers in a population can be determined. The fluctuations in numbers from year to year and the age composition of the population can be ascertained. A knowledge of the exact time at which changes in numbers occur, combined with a knowledge of the requirements and behavior of a species and of its ability to meet adverse conditions, should indicate the complex of factors that is effective in eliminating individuals. Kendeigh (1934) has broken the way for an analysis of the resistance of a species to varying external conditions. The requirements of a species with respect to amount and kind of food, nesting sites, and places of refuge are not difficult to determine, but the supply available in a given area is a problem of the first magnitude. Any study combining these lines of attack should give new insight into the factors that control avian populations, that govern the adjustment of species and environment, and that play a major part in selective adaptation.

### TERRITORY AND POPULATION

The behavior of the wren-tit in many respects fits the concept of territory as set forth by Howard (1920). The male seeks out and establishes himself in a limited area. He announces his presence in it and his song is reacted to by other wren-tits, both males and females. He is joined by a female and together they defend it from other wren-tits, and, in course of time, raise a brood within its limits.

But certain variations are evident. The periods of acquiring a territory and of seeking a mate, the first and second phases into which Howard (1929) divides the reproductive cycle, extend over a long period of time, at least for the species as a whole, and may to a greater or less degree overlap. This longer period, which is possible in a resident species, results in the finding of a territory or mate by most individuals, and lessens the severity of the competition between individuals. Once established, the pair, at the proper season, advances into the third phase, that of nest building and coition, and finally into the fourth, that of rearing young.

After the pair has nested, however, the territorial behavior of its members does not fade out. Rather than returning to the apparently sexless condition of many species in late summer, fall, and winter, they remain in a state similar to that of the second phase, so that at the following breeding season the reproductive cycle starts at this level and only the third and fourth phases are re-

peated. Normally, the first phase is never repeated. The male takes up a territory only once in his lifetime. The second, barring accident to the mate, also is not repeated. If the female dies, the second phase is repeated and the male obtains a new mate; if the male dies, the female joins another male.

As this study of wren-tits has shown specific peculiarities in respect to territorial habit, so intensive studies of other birds (European robin, Burkitt, 1924-1926; shrike, Miller, 1931; song sparrow, Nice, 1933-1934; corn bunting, Ryves and Ryves, 1934; Dartford warbler, Venables, 1934; western mockingbird, Michener and Michener, 1935) have shown other modifications, and more will unquestionably be found and are to be expected. Each species must meet the same general problems of individual and species survival, but each has different abilities and requirements which limit it in solving these problems. All have not solved them in the same way. When the complete pattern of behavior of at least representative types of birds, from the primitive to the specialized, solitary to colonial, is known, we may find infinite variations of a single fundamental pattern involving territory; or, possibly, a number of intergrading patterns.

The territorial habit limits the number of individuals in a given area. In Hamilton Gulch in the course of a year an average of twelve or thirteen locations was all that became available for about thirty-three young wren-tits. Whether or not possession of a territory is essential to the success of the individual life, it is unquestionably essential to reproduction. The ultimate competition is for space. Theoretically the minimum size of territory demanded by a wren-tit will determine the maximum number of individuals that can live in a given area. This theoretical limit is rarely if ever reached. The individuals present do not exert enough pressure to compress the territories to this minimum size. Since the individual holding a territory is almost without exception successful in its defense, only an unusually dominating individual can get a foothold in an occupied area. In each of the three years of field work, three or four individuals have failed to do so. Therefore the territorial habit is a basic factor, determining the density of a population, the operation of which is modified by various circumstances such as the number of new individuals produced, the percentage of these surviving to the next breeding season, the strength of the territorial habit in the surviving individuals, and the effect of environmental conditions on the territorial habit.

The territorial habit tends to keep the density of the population constant. The number of territories into which a given area can be divided will be approximately the same each year. Even when an exceptionally large number of individuals are produced, or survive to their first breeding season, the number that find places in which to breed will not be greatly increased. The potential geometric rate of increase is damped before it has a chance to get under way.

## A WREN-TIT'S LIFE

At hatching, a wren-tit is a blind angular mite which knows only to raise its head and open its bill at a jarring of the nest so that it may be nourished, and to carry out the reflexive act of evacuation, which is sometimes but not always stimulated by the parents. In two weeks the young bird has changed to a streamlined, bobtailed youngster that eagerly awaits and calls to its parents as they approach, that cares for itself to the extent of preening its feathers, that restlessly, in response to no evident external stimulus, stands up in the nest and vibrates its wings, that watches its surrounding world of tangled brush with interest, and that distinguishes and is stimulated by abnormal events therein. A day or two later it hops into its world of interlacing twigs.

The first hours out of the nest are a time of rapidly changing behavior patterns, for within that time the first uncontrolled state of continuous crying is replaced by the power to respond by motionless silence to the parents' alarm notes. The change in physical capacity is less rapid. The fledgling spends most of the time perched in a row with its brothers and sisters, where it clamors for food and greedily swallows what is brought. When in motion, it progresses by a series of short hops accompanied by a probably futile fluttering of the wings, but it is not sure-footed and if hurried often fails to gain its intended objective and scrambles desperately to recover its balance as it falls. Normally it covers only a few yards during the first days, though greater efforts may be made in response to fright.

Within four or five days, however, it hops through the brush with nearly the ease and skill of the adults and has the power of actual flight, though for a few feet only. For the next few weeks it shows two dominant preoccupations—to keep close to its parents, and to persuade them to feed it. It receives food from them at about the same frequency as during the last days in the nest. Needless to say, it has undergone a myriad of experiences with the elements of its environment and developed in many ways imperceptible to us.

By the time it is five or six weeks old the fledgling is fully feathered and flies readily, hunts at least some of its own food, helps its parents to scold an intruder, and is excited by, but probably does not take part in, disputes with neighboring families. Actual separation now begins, though very gradually. During the next four weeks it ceases to follow its parents as closely, perhaps less because of its reduced sense of dependence than because of their reduced interest or even resentment of its clamorous persistence—though on this my information is inadequate. Restriction to the home territory has evidently been through attachment to the parents, for with this bond weakened, the young bird, in seeking food, may go beyond the boundaries, and finally, when nine or ten weeks old, fails to return.

For a time it wanders freely, pausing wherever it finds food. It comes in contact with members of its own kind and may sometimes be weakly gregarious with any of them, but it distinguishes and is attracted by an individual of the opposite sex, and a young male and female wander together until sep-

arated by chance or a new interest. Such companions forage together, keep track of each other by calls, preen each other, and undoubtedly sleep together at night. The male occasionally utters a juvenile song. Such a foot-loose phase may terminate in a month or may last several months. This period may be one of curiosity, which makes for pioneering, or merely a period of complete indifference to locality and consequent drift, or nothing more than submission to rebuff after rebuff from landed birds until a place of temporary peace is found by trial and error. I suspect that the first suggestion contains more of the truth.

The next perceptible step toward maturity is the inclination which arises during the fall to remain in one place where, with its companion of the moment, it can subsist without being harassed by established birds.

Sometime in the course of the winter—certainly by March—the young bird ceases to be satisfied merely with a place to forage and a casual companion. The period of passive settlement gives way to an active phase which marks the arrival of maturity, beyond which change is cyclic and development stops. Here, on the threshold of maturity, sex as a dynamic force begins to operate and male and female behaviors diverge. The psychological effect of the physiological changes which are taking place is to concentrate the forces of the male not on the search for a mate, but on the acquisition of an adequate habitation, from which he excludes all other wren-tits except the female which he accepts. If he does not meet opposition and the area is suitable, he may stay where he has been content to remain passively for weeks or months, but if his rising ambition brings him into conflict with individuals on whose marches he has been tolerated, but in whom the same ambitions are fully developed, he is driven from his place of sojourn and can satisfy his desires only when he finds an area not defended by an established pair, or when his desire reaches the strength of theirs and he can meet their attacks and wrest a foothold from them. His success in obtaining a territory gives him the power to hold a mate, and opens the floodgates of song. The immediate interest of the female, on the other hand, is not primarily in ground, but in a male which possesses it, and as her desire grows she will leave a landless companion to join a male which holds a territory. Perhaps if her casual companion's desires keep pace with or are in advance of hers, she will remain with him and they will become established together.

At any rate, by the first of March the average wren-tit of either sex approaching one year of age is established on an estate of about .8 of an acre of chaparral, which it shares with its mate. Whatever the mental imagery may be, the male has formed from his passion for land and from his conflicts with like-minded neighbors a working concept of his territory as a whole and of its relation to those which surround it. With this has come the recognition of a female as his mate. His mate, though her interest in ground was secondary, has acquired the same working concept, and the energies of the two are harmonized and directed toward the defense of their estate and toward keeping in touch with each other.



Territorial possession and behavior are well established when, about the first of April, a series of new elements rapidly and for the first time burgeon in the minds of the birds and drive them through a maze of novel reactions to a degree of forced activity in strong contrast to the base level of life outside of the breeding period. They resent the presence of jays and mob them. They are excited by frayed bark surfaces or by cobweb, and collect fragments of both. Soon they are combining the two into a nest, and as it takes form, each finds satisfaction in sitting in it. Simultaneously their interest in each other builds up toward its peak, finds expression in the exciting chase of sexual flight, and finally, as the nest nears completion, reaches its climax in coition.

With egg laying begins a period of rigid and exacting routine, the pair being continually separated. Each takes its turn on the eggs, and between shifts finds food for itself, scolds intruders, and defends the territory, though as the season advances this is less frequently necessary, for the pairs have come to recognize their boundaries and are busy with their respective families. With hatching, the function of supplying food for the nestlings is added to the routine of the pair, but insects are abundant and the additional demand on time and strength seems to be met without excessive effort. As the nestlings reach the age at which they can be left most of the day without brooding, the pair, which for a month have been separated by alternating tasks, are again seen moving and working together.

Judged by their resentment of intruders and boldness in defense, the parents' concern increases with the growth of the young and reaches its peak when the latter leave the nest. Thereafter the adults are no longer tied to one spot, and as the young gain in mobility, the family moves as a unit. After a time, however, the interest of the parents in their offspring wanes until the adults no longer understand the importance of the young and perhaps finally resent their importunities or even their presence.

The successful rearing of a family releases the pair from the complex chain of activities it entails, but if the series is interrupted by the destruction of the eggs or young, bark fiber and cobweb again become objects of fascination and the cycle begins anew.

By the end of June at the earliest or the middle of September at the latest, the absorption of the parents in rearing young ends, and until the following spring their life continues on a relatively uniform level. Their activities serve only to maintain their own lives, their companionship, and their territory. They are constant companions, forage together, keep track of each other by calls, preen each other, sleep together, and may rarely show sexual excitement to the degree of attempting copulation. The male sings regularly, and both defend the territory from invasion. In the fall each molts, but this is a gradual process and, so far as I can see, does not change the tone of the bird's behavior, though more time is spent in preening. As the season advances, it is increasingly hard for the members of the pair to satisfy their own needs, but it is usually not beyond their power to do so. In the fall and early winter there occurs a subtle, indefinable, and very limited change, in effect a relaxation, in

the bird's preoccupation with its territory, an increased tolerance, a sense of the temporary harmlessness of invasion, evidenced by toleration of wandering young and even by rare excursions outside the territorial boundaries. Trespass by an immature bird whose territorial ambition is not developed does not bring out the defensive action called forth by one actually seeking establishment. With the approach of spring, as more and more young birds begin determined prospecting, the established pairs devote more energy to defense, but this probably correlates with the increasing danger rather than with any great fluctuation in territorial jealousy.

Finally, the pair become subject to the compulsions of the reproductive period and the annual cycle begins again. It may be repeated as many as ten times, but the survival of five cycles is the average success of the wren-tit.

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## EXPLANATION OF PLATES

### PLATE 9

Aerial view of Hamilton Gulch and its surroundings. California Schools for Deaf and Blind in foreground, Hamilton Gulch in center, Strawberry Canyon in background. Photograph taken in 1933 by Clyde Sunderland, Oakland, California.



## PLATE 10

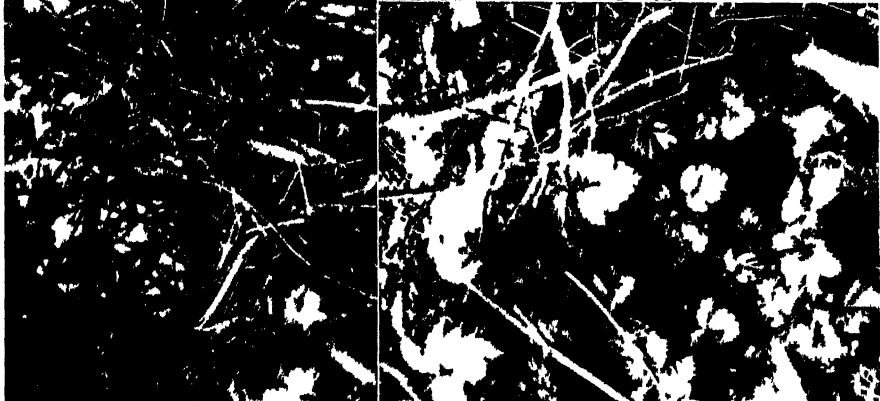
Aerial view of Hamilton Gulch. In the text, the path on the lower left hand slope is referred to as trail A, the lower road is road B, and the upper road as road C. Photograph taken in 1933 by Clyde Sunderland, Oakland, California.





PLATE 11

Wren-tit nests and nest sites. Upper left, unfinished platform in typical buchuus location. Photographed August 2, 1953. Upper right, finished nest in sticky monkey flower. Photographed August 4, 1953, after young had left. Lower left, nest (lower right corner) in blackberry tangle. Photographed May 6, 1951. Lower center, nest showing support in buchuus. Photographed June 14, 1953. Lower right, characteristic location in buchuus, nest under white signal. Photographed August 2, 1952.



## PLATE 12

Juvenile wren tits. Two upper and lower left, on day on which the young left the nest. Photograph taken August 2, 1933. Lower right, nestling four teen or fifteen days old. Photograph taken June 6, 1933.

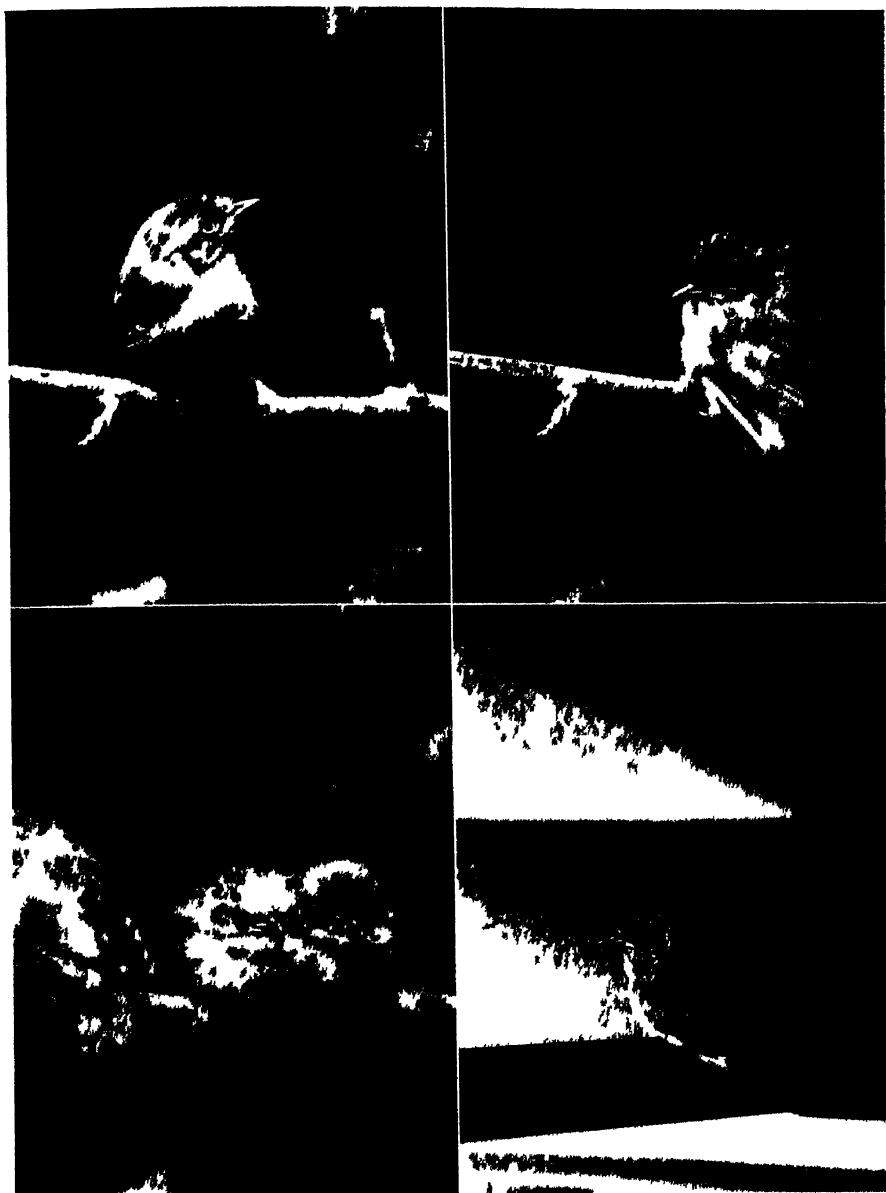


PLATE 13

Captive wren tits after having gone to roost at night. Photographs taken by C. A. Pease.



PLATE 14

*a* Roosting bush of male C41352 R and his mate  
Arrows indicate roosting perch. Photographs taken  
on May 6, 1931

*b*. Isolated brush patch which male C41352 R  
sought to utilize as a territory in 1931. Photograph  
taken May 6, 1931



b





A NEW PIKA  
(MAMMALIAN GENUS OCHOTONA)  
FROM SOUTHEASTERN IDAHO  
WITH NOTES ON NEAR-BY  
SUBSPECIES

BY

E. RAYMOND HALL AND H. LORRAINE BOWLUS

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# A NEW PIKA (MAMMALIAN GENUS OCHOTONA) FROM SOUTHEASTERN IDAHO, WITH NOTES ON NEAR-BY SUBSPECIES

BY

E. RAYMOND HALL AND H. LORRAINE BOWLUS

(Contribution from the University of California Museum of Vertebrate Zoology)

AN ATTEMPT to identify pikas recently taken in Idaho by Dr. William B. Davis led us to study the kinds of *Ochotona* previously named from Idaho and adjoining regions. Results of our study include the recognition of a heretofore unnamed race, and the finding of previously unrecorded geographic variations in subspecies from near-by areas, as set forth below.

## *Ochotona princeps clamosa* new subspecies

*Type*.—Male, adult, skin and skull; no. 78100, Mus. Vert. Zoöl.; N rim Copenhagen Basin, 8400 ft., Bear Lake County, Idaho; July 21, 1937; collected by William B. Davis; original no. 2645.

*Range*.—Bear River Range of southeastern Idaho.

*Diagnosis*.—Size: medium (see Measurements). Color: dark; in fresh summer pelage, near (c) Light Ochraceous-Buff (capitalized color terms after Ridgway: Color Standards and Color Nomenclature, 1912) mixed with blackish, the latter color predominating; underparts whitish washed with near (c) Pinkish Buff. Skull: auditory bullae much inflated; palatal bridge narrow, with anterior border anteriorly concave; lateral margins of nasals straight; interpterygoid space spatulate.

*Comparisons*.—*Ochotona princeps clamosa* resembles *O. p. ventorum* and *O. p. goldmani* more closely than it does *O. p. vinta* and is judged to be about as closely related to *goldmani* as to *ventorum*. The size is about as in *ventorum* or *vinta* and greater than in *goldmani*. The color below and in worn winter pelage is nearest to that of *goldmani*, but that of the fresh summer pelage is nearest to *vinta* though intermediate toward *goldmani*. The auditory bullae are more inflated than in adjoining races. The palatal bridge is narrower than in *vinta* and about as in *goldmani* and *ventorum*. The anterior margin of the palatal bridge is broadly V-shaped as in *goldmani* and *ventorum*, and not straight as in *vinta*. The lateral margins of the nasals are straight as in *goldmani* rather than concave as in *ventorum* and *vinta*. The interpterygoid space is spatulate, or at any rate narrower posteriorly, as in *ventorum*, rather than parallel-sided as in *goldmani* and *vinta*.

*Remarks*.—The greater inflation of the auditory bullae in *clamosa* than occurs in near-by races is reflected in the following measurements of the distance to which the bullae project below the basioccipital in three of the subspecies studied. Average and extreme measurements in millimeters are as follows: *O. p. clamosa*, 4.5 (4.2–4.9); *ventorum*, 3.7 (3.4–4.0); *goldmani*, 4.0 (3.8–4.4); *vinta* from Summit County, 4.2 (4.1–4.3). The greater inflation in *clamosa* is apparent also in the horizontal plane.

If Howell's (N. Am. Fauna, no. 47, 1924) arrangement of the pikas were followed, *clamosa* might best be treated as a subspecies of the species *schisticeps*. However, in conformity with the findings of Borell (Jour. Mammalogy, vol. 12, p. 307, 1931) that all the kinds previously treated as subspecies of *schisticeps* and *princeps* may be arranged as subspecies of *Ochotona princeps*, *clamosa* is treated as a subspecies of *princeps*.

The three specimens from Deep Lake, only 15 miles or so south of the type locality of *clamosa*, are slightly lighter colored than *clamosa* and, so far as the damaged skulls permit one to judge, have the interpterygoid space less spatulate. These variations are tendencies toward the conditions obtaining in *winta*.

*Specimens examined*.—Total number 22, all from Idaho, as follows: Bannock County:  $\frac{1}{4}$  mi. W Copenhagen Valley, 8400 ft., 1 (Mus. Vert. Zoöl.). Franklin County: 2 mi. E Strawberry Creek Ranger Station, 8500 ft., 2 (Mus. Vert. Zoöl.). Bear Lake County: N rim Copenhagen Basin, 8400 ft., 16 (Mus. Vert. Zoöl.); Deep Lake, Bear River Mountains, 3 (Brigham Young Univ.).

Study of the specimens available to us makes it possible to offer revised diagnoses of some earlier named races, as follow.

### *Ochotona princeps uinta* Hollister

1912. *Ochotona uinta* Hollister, Proc. Biol. Soc. Wash., vol. 25, p. 58. April 13, 1912.

*Type locality*.—Uinta Mountains, near head of east fork of Bear River [Summit County], Utah (see Howell, N. Am. Fauna, no. 47, p. 19, 1924).

*Range*.—The Uinta and Wasatch mountain ranges in Utah.

*Diagnosis*.—Size: medium (see Measurements). Color: light, in both winter and summer pelage near (c) Pinkish Buff above with wash of same color on underparts. Skull with auditory bullae of medium size; palatal bridge of medium width with its anterior margin straight; lateral margins of nasals concave; interpterygoid space parallel-sided.

*Comparisons*.—Differs from *ventorum* in darker color, slightly more inflated auditory bullae, wider palatal bridge, the anterior margin of which is straight rather than anteriorly concave, and in having the interpterygoid space parallel-sided rather than spatulate. Differs from *figginsi* in lighter color (less reddish), wider palatal bridge the anterior border of which is straight rather than anteriorly concave, and in having the interpterygoid space parallel-sided rather than spatulate. Differences from *clamosa* noted in account of that race.

*Remarks*.—For size, color in summer pelage, and cranial characters the specimens from Summit County, Utah, are relied upon as typical of *winta*. The specimens from Mount Timpanogos are grayer than animals from Summit County, have the lateral borders of the nasals sometimes straight rather than always concave, and the anterior margin of the palatal bridge not straight but, instead, slightly concave anteriorly (though less so than in *goldmani* and *ventorum*), and the skull broader interorbitally. The populations from Daggett County, in comparison with *winta* from Summit County, likewise are grayer, and have skulls that are broader interorbitally with a wider palatal bridge. Indeed, in these pikas from Daggett County the palatal bridge is wider than in any others here reported upon.

Specimens from Bald Peak, only 12 miles southwest of the type locality, are in fresh summer pelage (July 15 and 19) and in color are almost the same as a topotype (U. S. Nat. Mus. no. 9749) in fresh winter pelage. Howell's (*op. cit.*, p. 20) statement that "it is the most uniformly buffy-colored race of all the American forms" probably had reference to the coat color on different parts of the body, but is applicable also to the coat color in different seasons.

*Specimens examined*.—Total number, 35, all from Utah, as follows: Summit County: Morehouse Canyon, 8500 ft., 5 mi. above Weber River, 3 (Univ. Utah, Dept. Zoöl.); SW slope Bald Mountain, 10500 ft., 5 (Mus. Vert. Zoöl.); Uinta Mountains, 2 (U. S. Nat. Mus., one in Biol. Surv. Coll.); near head of east fork of Bear River, 1 (U. S. Nat. Mus.). Dag-

gett County (unless otherwise noted, in Mus. Zool., Univ. Michigan): Granite Park, 24 mi. S Manila, 2; The Nipple, 11000 to 11500 ft., 14; Spirit Lake, 1; Elk Park, 2 (Brigham Young Univ.). Utah County, Mount Timpanogos (Brigham Young Univ.): Aspen Grove, 2; Hidden Lake Cirque, 2.

### *Ochotona princeps ventorum* Howell

1919. *Ochotona uinta ventorum* Howell, Proc. Biol. Soc. Wash., vol. 32, p. 106. May 20, 1919.

*Type locality*.—Fremont Peak, Wind River Mountains, Wyoming (see Howell, N. Am. Fauna, no. 47, p. 18, 1924).

*Range*.—Salt River Range and Wind River Range, north to the Beartooth and Absaroka ranges in southern Montana, and in the Big Horn Mountains of north central Wyoming (modified from Howell, *loc. cit.*).

*Diagnosis*.—Size: medium (see Measurements). Color: pale in both winter and summer pelage; summer pelage above, Cinnamon-Buff to Pinkish Cinnamon with trace of blackish; underparts washed with Cinnamon-Buff; auditory bullae relatively uninflated; palatal bridge narrow, with anterior border anteriorly concave; lateral margins of nasals concave; interpterygoid space spatulate.

*Comparisons*.—Differs from *figginsi* in much lighter color, in longer nasals, rounded posteriorly rather than truncate, and in slightly larger auditory bullae. For comparison with *uinta*, *goldmani*, and *clamosa* see accounts of those races.

*Remarks*.—The pikas from the Salt River Mountains, though intermediate toward *uinta* (specimens from Summit County, Utah), definitely show greater resemblance to *ventorum* as known to us by specimens from Lake Fork in the Wind River Mountains. The specimens from the Salt River Mountains differ, so far as we can see, only in slightly darker color, in more inflated auditory bullae, and in having the lateral borders of the nasals straight rather than concave.

*Specimens examined*.—Total number, 28, all in the U. S. National Museum, Biol. Surv. Collection, from Wyoming, as follows: Fremont County: Lake Fork, 9500 ft. to 11800 ft., 13. Lincoln County, Salt River Mountains: Head of Dry Creek, 9000 ft., 2; Dry Creek, 7500 ft., 1; 10 mi. SE Afton, 7000 to 9000 ft., 3; head of Smiths Fork, 3; LaBarge Creek, 9000 ft., 5; Salt River, 16 mi. S Afton, 1.

### *Ochotona princeps goldmani* Howell

1924. *Ochotona schisticeps goldmani* Howell, N. Am. Fauna, no. 47, p. 40. August 21, 1924.

*Type locality*.—Echo Crater, Snake River Desert, Butte County, Idaho.

*Range*.—Known only from Craters of the Moon National Monument, Idaho.

*Diagnosis*.—Size: small. Color: dark; predominantly blackish above with tinge of near (c) Light Ochraceous-Buff. Skull with auditory bullae well inflated; palatal bridge narrow, with anterior border concave anteriorly; lateral margins of nasals straight; interpterygoid space parallel-sided.

*Comparisons*.—*O. p. goldmani* differs from *ventorum* in smaller size, darker color, more inflated auditory bullae, and in having the interpterygoid space parallel-sided rather than spatulate. For comparison with *clamosa* see account of that race.

*Remarks*.—As pointed out by the original describer, this is the darkest American pika. It is, however, only slightly darker than *O. p. clamosa*, which, in some other features also, tends to bridge the gap between *goldmani* and the subspecies to the eastward.

AVERAGE AND EXTREME MEASUREMENTS, IN MILLIMETERS, OF ADULTS OF *Ochotona princeps*

| Specimens                                     | Total length  | Length of hind foot | Occipitomassal length | Zygomatic breadth | Breadth of brain case | Interorbital breadth | Width of palatal bridge | Length of nasals |
|-----------------------------------------------|---------------|---------------------|-----------------------|-------------------|-----------------------|----------------------|-------------------------|------------------|
| <i>O. p. goldmani</i> —3 ♂♂; Butte Co. ....   | 178 (164-182) | 30.5 (30.0-31.0)    | 42.6 (41.8-43.5)      | 20.6 (20.3-21.0)  | 18.4 (18.0-18.8)      | 5.6 (5.0-6.0)        | 2.0 (1.3-2.4)           | 13.5 (13.4-13.5) |
| <i>O. p. elmorei</i> —9 ♂♂; topotypes. ....   | 193 (175-205) | 32.3 (30.0-34.0)    | 43.7 (40.0-45.0)      | 21.8 (21.1-22.5)  | 18.6 (17.6-19.2)      | 5.5 (5.2-5.8)        | 2.0 (1.7-2.5)           | 14.9 (13.7-15.8) |
| <i>O. p. ventorum</i> —5 ♂♂; Lake Fork. ....  | 195 (173-204) | 31.0 (30.0-32.0)    | 44.0 (41.2-46.3)      | 22.1 (22.0-22.3)  | 18.0 (17.5-18.5)      | 5.3 (4.9-5.7)        | 2.3 (2.0-2.8)           | 15.1 (13.6-15.6) |
| <i>O. p. ventorum</i> —5 ♂♂; Lincoln Co. .... | 194 (170-196) | 31.2 (30.0-32.0)    | 43.5 (41.5-45.2)      | 21.4 (20.9-21.7)  | 17.7 (16.5-18.8)      | 5.2 (4.8-5.7)        | 2.2 (2.0-2.5)           | 14.4 (13.3-15.5) |
| <i>O. p. winteri</i> —4 ♂♂; Summit Co. ....   | 195 (175-210) | 29.5 (29.0-30.0)    | 45.3 (45.0-45.6)      | 21.7 (21.4-22.1)  | 18.4 (17.8-18.7)      | 5.2 (4.9-5.5)        | 2.7 (2.3-3.5)           | 15.3 (15.1-15.6) |
| <i>O. p. winteri</i> —2 ♂♂; Utah Co. ....     | 195, 195      | 33.0, 32.0          | 49.9, 44.4            | 21.3, 22.0        | 18.5, —               | 5.4, 5.6             | 2.2, 2.6                | 15.9, 15.4       |
| <i>O. p. winteri</i> —6 ♂♂; Daggett Co. ....  | 185 (175-220) | 31.6 (29.5-34.0)    | 46.7 (44.1-50.3)      | 23.0 (22.3-24.6)  | 18.9 (18.0-20.5)      | 5.7 (5.3-5.8)        | 2.9 (2.6-3.0)           | 16.4 (15.9-17.7) |
| <i>O. p. agnatus</i> —8 ♂♂; topotypes. ....   | 183 (171-196) | 30.9 (27.4-33.0)    | 43.3 (42.8-43.9)      | 21.7 (21.3-21.9)  | 17.4 (17.4- ...)      | 5.2 (4.9-5.4)        | 2.3 (2.0-2.9)           | 14.5 (14.2-15.2) |
| <i>O. p. goldmani</i> —4 ♀♀; Butte Co. ....   | 177 (165-183) | 30.3 (30.0-31.0)    | 41.6 (39.7-43.9)      | 20.6 (19.8-21.6)  | 17.3 (16.2-18.7)      | 5.7 (5.4-6.1)        | 2.0 (1.8-2.1)           | 12.9 (12.4-13.4) |
| <i>O. p. elmorei</i> —6 ♀♀; topotypes. ....   | 191 (157-195) | 32.0 (30.0-33.0)    | 43.1 (41.6-44.5)      | 20.5 (20.4-20.8)  | 17.5 (17.2-18.4)      | 5.2 (5.0-5.6)        | 1.9 (1.7-2.0)           | 14.6 (13.9-15.1) |
| <i>O. p. ventorum</i> —4 ♀♀; Lake Fork. ....  | 202 (153-215) | 31.0 (30.0-32.0)    | 44.5 (43.5-46.5)      | 21.4 (21.3-21.6)  | 18.3 (17.5-19.0)      | 5.1 (4.9-5.5)        | 1.9 (1.7-2.0)           | 14.8 (14.1-15.4) |
| <i>O. p. ventorum</i> —4 ♀♀; Lincoln Co. .... | 194 (190-200) | 31.0 (30.0-32.0)    | 43.3 (43.2-43.7)      | 21.3 (20.8-21.8)  | 18.2 (17.7-18.7)      | 5.1 (4.8-5.8)        | 1.9 (1.7-2.0)           | 14.5 (14.1-14.9) |
| <i>O. p. winteri</i> —3 ♀♀; Summit Co. ....   | 151 (177-157) | 30.3 (25.0-32.0)    | 44.1 (43.3-45.4)      | 22.0 (21.7-22.4)  | 17.7 (17.6-17.8)      | 5.3 (5.1-5.6)        | 2.7 (2.4-3.0)           | 15.1 (14.5-15.8) |
| <i>O. p. winteri</i> —2 ♀♀; Utah Co. ....     | 153, 195      | 30.0, 32.9          | 42.9, —               | 21.9, 20.6        | 18.1 —                | 5.6, 5.6             | 2.4, 2.8                | 14.6, 14.4       |
| <i>O. p. winteri</i> —7 ♀♀; Daggett Co. ....  | 192 (164-210) | 30.0 (28.5-31.5)    | 45.3 (43.6-46.7)      | 22.0 (21.6-22.9)  | 18.1 (17.6-18.7)      | 5.6 (5.5-5.7)        | 3.1 (2.7-4.3)           | 15.7 (15.0-16.3) |
| <i>O. p. agnatus</i> —3 ♀♀; topotypes. ....   | 154 (175-197) | 29.0 (23.4-30.1)    | .....                 | 21.1 (20.9-21.5)  | 17.7 ( ... )          | 5.2 (5.1-5.3)        | 2.3 (1.8-2.6)           | 13.8 (13.5-14.1) |

*Specimens examined.*—Total number 5, Craters of the Moon National Monument, in Butte County, Idaho, in the Museum of Vertebrate Zoölogy, as follows: south base of Grassy Cone, 5900 ft., 4; Great Owl Cavern, 5877 ft., 1.

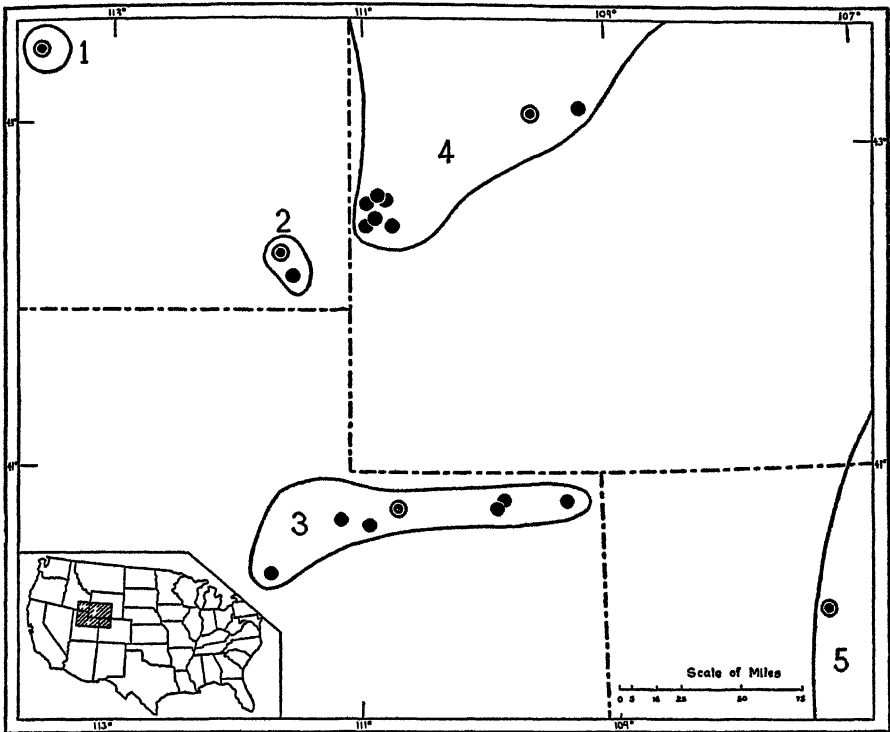


Fig. 1. Map to show geographic ranges within area studied, of five races of *Ochotona princeps*. Dots indicate localities from which specimens have been examined. Type localities are circled. 1, *Ochotona princeps goldmani*; 2, *O. p. clamosa*; 3, *O. p. uinta*; 4, *O. p. ventorum*; 5, *O. p. figginsi*.

### *Ochotona princeps figginsi* J. A. Allen

1912. *Ochotona figginsi* J. A. Allen, Bull. Am. Mus. Nat. Hist., vol. 31, p. 103. May 28, 1912.

*Type locality.*—Pagoda Peak, Itio Blanco County, Colorado.

*Range.*—Western Colorado from Gunnison County north to Bridger Peak, Carbon County, Wyoming (after Howell, N. Am. Fauna, no. 47, p. 21, 1924).

*Diagnosis.*—Size: medium (see Measurements). Color: upper parts in summer pelage near (12") Vinaceous-Cinnamon, washed with same color below. Skull: auditory bullae moderately inflated; palatal bridge of medium width, with anterior border concave anteriorly; nasals truncate posteriorly, with lateral margins concave; interpterygoid fossa spatulate.

*Comparisons.*—For comparison with *ventorum* and *uinta* see accounts of those races.

*Specimens examined.*—Total number, 12, topotypes from collection of Colorado Museum of Natural History.

Transmitted June 25, 1938.





STRUCTURAL ADAPTATIONS IN  
THRASHERS  
(MIMIDAE: GENUS TOXOSTOMA)  
WITH COMMENTS ON  
INTERSPECIFIC RELATIONSHIPS

BY  
WILLIAM L. ENGELS

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Fig. 1 Palmer curve-billed thrasher (*Toxostoma curvirostre palmeri*) in a typical pose.  
Photographed at G. Hofer's homestead, near Tucson, Arizona,  
by A. H. Miller, June 6, 1956.

# STRUCTURAL ADAPTATIONS IN THRASHERS (MIMIDAE: GENUS TOXOSTOMA) WITH COMMENTS ON INTERSPECIFIC RELATIONSHIPS

BY

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(Contribution from the University of California Museum of Vertebrate Zoology)

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## INTRODUCTION

IN THE past few decades, vertebrate anatomy, having forsaken in large part the investigation of homologies and the phylogenetic relationships of major taxonomic groups, has embarked upon a new course and is seeking to expose the fundamental anatomical mechanisms underlying the habits of animals. It has thus become dynamic; one of its most vigorous proponents has termed it "biologische Anatomie" (Böker, 1924). It seeks a fresh, detailed knowledge of structural adaptation, of correlation between form and function, between structure and habit, in the belief that such knowledge will lead to the establishment of principles governing the development of form, that is, of morphology in its broadest and most significant meaning.

In the traditional comparative anatomy of the post-Darwinian period, such marked resemblance in form as is manifested by sharks and porpoises, to take an extreme example, was only confusing, since it tended to obscure those homologies for which anatomists sought in order to establish phylogenies, and in the conception of which function (habit) played no part. Today, it is recognized that the factors which bring about the striking similarities in form which animals of the most diverse phylogenetic history often present are as significant for the understanding of morphology as homologies are significant in the establishment of phylogeny.

For a full understanding of adaptations, however, phylogeny cannot be lost sight of, since the factors, whatever they may be, which come into play at any given time in the development of form, have an inherited body of material to work upon, the nature of which varies according to its phylogenetic history. Therefore it is desirable, in investigating the adaptational significance of an anatomical mechanism in any species, to inquire about its distribution and functional correlation in closely related species. This paper presents the results of an attempt to investigate structural adaptations in this manner, an attempt, that is, to make a comparative study of form and function among the species of a single genus.

The species of birds which provide the principal material for this study are the thrashers. They comprise the genus *Toxostoma*, one of thirteen genera making up the distinctly New World family Mimidae (the mockingbirds).

The genus includes ten species, ranging through temperate and subtropical North America; it is most abundantly represented on the deserts of southwestern Arizona and the adjacent parts of Mexico, where four species occur over common territory.

The genus includes birds widely different in general appearance, both in structure and in behavior. The brown thrasher (*Toxostoma rufum*) of the eastern United States and Canada is thrushlike in aspect; the bill is straight, moderately long; the upper parts of the bird are dull rufous in color, the lower parts pale buff, and the chest, sides, and flanks are streaked broadly with dark brown. The California thrasher (*Toxostoma redivivum*) appears to have few characters in common with the brown thrasher: the bill is very long and markedly decurved, sicklelike; the bird's upper parts are grayish brown and the underparts somewhat lighter in color, but without the dark streaks so distinctive of the brown thrasher. The migratory brown thrasher, in its daily rounds, progresses predominantly by flight; the nonmigratory California thrasher is a swift and skillful runner and makes little use of its wings in moving about. Other species of the genus are intermediate in various respects between these two extremes. The thrashers therefore recommend themselves as objects peculiarly suited to a study in dynamic avian anatomy—a comparative study of structure with special reference to adaptation.

In practice, I have approached the problem of correlating peculiarities of structure with peculiarities of behavior from both sides; that is, the existence of distinctive habits has been inferred from anatomical study and this has been followed by a search for these habits in field studies; and, vice versa, anatomical peculiarities have been sought out, the presence of which was suggested by observed behavior. In stating the results, however, it seemed to me preferable to use behavior as a background against which the anatomical picture may be viewed.

#### MATERIALS

Twelve species in six genera of the Mimidae are represented among the 209 skeletons of adult birds which have been available to me in the course of this study; these include seven species of *Toxostoma*, represented by 139 skeletons. I have also had at hand alcoholic specimens of twelve species in five mimid genera, including six species of *Toxostoma*. In addition, the collection of bird skins in the Museum of Vertebrate Zoölogy has been constantly at my disposal.

#### ACKNOWLEDGMENTS

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## USE OF BILL AND METHODS OF LOCOMOTION IN THRASHERS

All thrashers are rather shy birds, and any attempt at spying out intimate details of their daily life must tax severely the patience and time of the observer. The task is not lightened by restricting it, as I have done, to observing those aspects of behavior which have to do with the use of the bill and the methods of locomotion, since many hours in the field may reward one with but fleeting glimpses of foraging individuals.

The following notes are not intended to be exhaustive; they indicate, in a broad manner, similarities and differences in some habits of the six species of thrashers which I have studied in the field.

The California thrasher (*Toxostoma redivivum*), which occurs in the chaparral on the hills and in the canyons immediately about Berkeley, was watched from time to time during 1935 and 1936, although relatively continuous observations were made only during the spring of 1935. In mid-December of 1934 three days were spent in the southern part of the San Joaquin Valley of California, with A. H. Miller and R. M. Eakin, for the purpose of collecting Leconte thrashers (*Toxostoma lecontei*); some observations on methods of locomotion in this species were made at that time. In the early summer of 1936 (May 24-June 7), in company with Dr. Miller, I visited the Santa Cruz Valley region in Arizona, where Bendire (*Toxostoma bendirei*), Palmer curve-billed (*Toxostoma curvirostre palmeri*), crissal (*Toxostoma dorsale*), and Leconte thrashers occur abundantly. More than one hundred thrashers were collected in this period; almost every day at least a few birds of each of these species were seen and numerous opportunities were afforded us to compare their behavior with respect to locomotion. On a few occasions it was possible to watch also their methods of foraging and their use of the bill. From Arizona I went directly to Wisconsin; there, at intervals in a six weeks' period, these same aspects of behavior were studied in the brown thrasher (*Toxostoma rufum*). The observations made at these various times, supplemented by information found in the literature, form the basis for the following accounts of species.

*Toxostoma rufum*.—Like other thrashers, this species probably never seeks food material by scratching, although most of its foraging is done on the ground. The bill is the important, if not the sole foraging tool. With its bill



the brown thrasher pokes among such ground litter as dead leaves and twigs in search of insects and fallen seeds and berries. Frequently the bill is thrust into the ground with repeated sharp blows; presumably, insects, grubs, and worms are sought in this way. F. H. Test has informed me that he saw a brown thrasher hammer vigorously with its bill at a sunflower seed which it had picked up and laid down again on the ground; the bird treated a number of seeds in the same fashion on this occasion. The movement of the head and bill is mostly a straight up-and-down movement, with little or no sweeping from side to side; litter is sometimes whisked about with side-to-side movements.

When on the ground, the brown thrasher moves along quickly, walking or running with short, easy strides. I once saw one, in the early morning, foraging over a thick lawn for insects, which it caught by hopping forward and striking out at the same time with the head and neck. In moving about in its foraging, this bird hopped at least as frequently as it walked, sometimes covering several feet in a series of quick hops. This hopping was not seen in any other brown thrasher; but the grass of the lawn this one was covering was rather high, thick, and wet with dew, and presumably hindered free walking. In walking or running, the tail is carried relatively low; at least it does not stand up at a sharp angle from the back.

In moving from place to place, as from one forage area to another, or between forage area and nest site, the brown thrasher usually flies. Its flight is strong and even, often ending in a glide and a swoop, either upward into tree or bush, or downward to the ground. On several occasions when adults were observed feeding fledged juveniles, the young were perched in trees or bushes, and the old birds came to them each time on the wing.

The importance of flight in the locomotion of the brown thrasher is heightened by its semiannual migrations. The winter range of the species, which extends from "southeastern Missouri and North Carolina to central southern Texas [and] central Florida" (Hellmayr, 1934, p. 295), overlaps to the north the southern portion of the breeding range. Whether some individuals in this region are resident is not known; certainly the more northern-breeding birds make a migration of at least six hundred miles.

*Toxostoma bendirci*.—The Bendire thrasher, like the brown, spends much time on the ground while foraging. Near Coolidge, Arizona, one was watched from an automobile as it searched for food on the shoulder of the road, hammering vigorously at the ground with its relatively short, slightly curved bill. Another, seen in a cultivated field beside a patch of mesquite in which its nest was situated, was running along between plant rows, occasionally jumping up into the air as if catching insects. Near Florence, Arizona, on a creosote-bush flat, I saw one acting in a somewhat similar manner; I followed it several hundred yards. It walked or ran along, now slowly, now rapidly, in and out among the creosote bushes, sometimes flying up into a low bush, then directly down again to the ground. Gait and carriage in these birds were essentially as in the brown thrasher.

Most Bendire thrashers seen, when not perched, were moving on the wing

in smooth easy flight. A. H. Miller (MS field notes, 1936) finds their flight remindful of that of mockingbirds. Flight is their usual method of locomotion; time and again they were seen flying from tree to tree at heights of from twenty-five to fifty feet, and, once, for a distance of more than a quarter-mile. This behavior was especially noticeable when the bird was being pursued; before I could maneuver myself into shotgun range, the bird would fly off to some more distant perch. A bird suddenly approached, while on the ground, flew directly up into the top of an adjacent mesquite about thirty feet high. On another occasion, when I was well hidden near a mesquite in which was a nest with young, I saw the male parent come flying into the top of the rather high tree, then begin to work down toward the nest about fifteen feet below. An hour later the female approached in a similar manner. Each was collected in turn and was found to be carrying small, green, wormlike larvae. These birds were approaching the nest from a cultivated field some three hundred yards away, in which, several times, I had seen Bendire thrashers foraging. It seems certain that this pair traveled that entire distance on the wing many times each day during the breeding period.

Observers have not been of one mind in attributing migratory habits to the Bendire thrashers. Scott (1886, p. 257) mentions this species as being migratory, but offers no details. Brown (1901, p. 225) is more definite: "... during the winter months an occasional one can be found in their usual habitat, but as a whole, they go south bodily on the first fall storm of wind or rain. The return migration is more gradual, but always of uncertain date."

Gilman (1909, p. 50), writing from Sacaton, Arizona, believed that all four members of the genus *Toxostoma* breeding there are resident species. "Some of them may leave for a short time in the fall, but there seems to be no regular migration. Bendire in particular seems to be scarce in the latter part of September and during October and November, but is occasionally seen during all that time. It is probably its dormant period, to recuperate from the molt."

But Howell (1916, p. 213) feels that "the prevailing impression is erroneous which regards the Bendire Thrasher . . . as a permanent resident of this locality. The section between Tucson and Fort Lowell is a favorite place to collect eggs of the species, but, although I kept careful watch, I saw only one bird (February 1) until March 17 when I secured another, and after which I saw two or three more. F. C. Willard offers evidence corroborative of this, as he tells me that the species occurs at Tombstone, the elevation of which is about twice that of Tucson, only during the winter [*sic*; summer ?]."

A. H. Miller (MS field notes, 1934-1935) failed to find Bendire thrashers near Continental, Arizona, during late December and early January. Together with Loye Miller, he worked the region thoroughly for three days, with the special purpose of collecting this species, and saw none; yet Loye Miller was able to point out areas there in which Bendire thrashers had been taken in the breeding season. This experience accords with Howell's and leads to a similar conclusion.

Hellmayr (1934) describes the range of this species as extending to northern

Sonora, but in winter "south to northern Sinaloa." The length of the migration route is thus probably less than that of the brown thrasher.

*Toxostoma curvirostre palmeri* (fig. 1, frontispiece).—The Palmer curve-billed thrasher, when ground foraging, uses its bill for hammering at hard objects of food or for exposing food materials hidden under debris or in the ground. One partly tamed bird observed at G. Hofer's homestead near Tucson, Arizona, which came to feed on dry bread thrown out on the ground, broke up a crust into crumbs of suitable size by hammering at it vigorously with its bill, much in the manner of a jay, but without holding down the crust in any way. This action was probably similar to that of the brown thrasher hammering at sunflower seeds. It is not an uncommon experience to see a Palmer thrasher pounding its bill into soft sandy ground with rapidly repeated downstrokes of the head, and with occasional side-to-side movements. Stafford (1912, p. 363) observes: "... my birds spend much time in the yard half squatting, with braced feet, digging holes of considerable depth (some as deep as two and a half inches) with quick, powerful blows of their sickle-like beaks; or casting aside the mould and parched soil with nervous sidewise thrusts, in search of grubs. On those parts of the desert, too, affected by the birds the ground usually shows plentiful signs of their probing."

The use of the bill made by Palmer thrashers thus apparently differs slightly from that of the brown and Bendire, which probably do not resort to digging. With respect to locomotion on the ground, another slight difference is to be noted. The gait of the Palmer thrasher is not smooth, but rather jerky; the bird gives the appearance of being set back on its haunches and of being stiff legged. The jerkiness of the gait is most in evidence when the bird is moving directly toward or directly away from the observer; the stiff-leggedness and the peculiar set of the body on the legs are best observed in profile. I do not mean to intimate that the Palmer thrasher is not at ease on the ground, but only that in its walking and running its action is not so smooth as that of other thrashers.

In mode of flight, the close observer may detect differences between the Bendire and Palmer thrashers. Gilman (1909, p. 50) observes that the flight of the Palmer thrasher is jerky, rather than smooth and even as is that of the Bendire. A. H. Miller (MS field notes, 1936) compares the flight of the Palmer thrasher to the "heavy boring carriage of the shrike," that of the Bendire to the "circular light beat of a mocker."

However, the Palmer thrasher is entirely like the brown and the Bendire in frequency of flight. In sixteen days on the Arizona deserts in 1936, I saw at least one hundred Palmer thrashers and followed many of them. Their reaction to pursuit was invariably the same; they moved away by flying, at a good height and often for rather long distances. On a cut-over mesquite flat one bird was followed for more than a half-mile, and in the course of its flight it entered and left four or five mesquites in succession without once descending to the ground. Brooding birds were repeatedly flushed from their nests in the cholla cactus; they always left on the wing and continued in flight to some

distant perch. One morning I visited a number of nests to collect nestlings and in my field notes for that day (May 26) wrote: "... as soon as we handled the young and they began to call, the old birds would shortly be heard calling in the distance, and soon seen, circling around from the top of one sahuaro to another, or to an ironwood tree or palo verde, where they would perch and call, gradually working nearer. . . . This approach was always via air. Once the birds began to call, and we had located them, we could follow them all the time, and they never went down to the ground, but flew from perch to perch."

Unlike the brown and Bendire, the Palmer thrasher is nonmigratory.

*Toxostoma redivivum*.—The California thrasher is a "habitual forager beneath dense and continuous cover. Furthermore, probably two-thirds of its foraging is done on the ground" (Grinnell, 1917, p. 432). The food which it obtains from the ground and surface debris beneath the chaparral cover is procured entirely by means of the long, curved bill. The feet are never employed for scratching, but ground spiders, grubs, and crickets are dug out of the ground; the curved bill is struck into the ground with rapid strokes of the head and neck, and the dirt "hooked" back and out with a powerful pull of the neck. Side-to-side sweeps of the bill are also frequent in the digging operation, but most of the dirt is thrown backward. Rather large objects may be thus moved; I once saw a California thrasher toss a clod of dirt half the size of my fist a distance of nearly two feet.

The bill is not always kept closed during the digging operation; the mandibles are frequently separated by a few millimeters, being then driven into the ground like a two-pronged fork rather than like a single pick. This was seen more often in the "hooks" and "pulls" than in the "lateral sweeps." Once an opening is made in the ground surface, many direct downthrusts or pokes are made. When digging, the bird frequently stops, cocks its head far to one side, bringing one eye to bear directly on the work, and seems to peer into the excavation.

In digging, especially if the action be vigorous, the feet are noticeably wide-spread, the legs bent sharply outward at the intertarsal joint, one foot often slightly in advance of the other. The bird thus widens its base and, grasping the ground firmly, obtains a more solid purchase. Not only are the legs bent outward, distally, but the proximal segments are bent upon themselves, the body springing upon them with the strong and rapid thrusts of the head and neck. With each thrust, also, the tail is jerked sharply to one side. Thus, all parts of the body except the wings are brought into play in this operation, each contributing its share to the sum of the forces which produce the powerful digging strokes and the return of the body to an easy, balanced position.

When the bird is foraging in surface debris, the actions are essentially the same, perhaps not so vigorous or powerful, but often sufficiently so to throw a shower of leaves or needles a distance of from three to four feet.

The chief organs of locomotion are not the wings, but the legs; and the avenues of travel are two: on the ground, and through the bushes. On the ground, a California thrasher both hops and runs; usually it runs, with long,

easy, rapid strides, but often, after it has traveled several feet in what seems to be straight running, there is a peculiar break in the pace and rhythm, followed again by straight running. While it is traveling along the ground, the tail is held up at a sharp angle, almost approaching the vertical; the head and forepart of the body are low. When it stops, the head and neck are raised and the bird assumes an erect position.

The California thrasher is also extremely agile in the bushes and trees, hopping or jumping from one twig or branch to another; in this manner it makes its way not only up and down in the same bush, but also from one bush to the next. In this mode of progression the long tail seems to play an important rôle, especially in climbing; as the forepart of the body is brought up preparatory to an almost vertical upward leap, the tail is depressed; it is sharply raised again as the branch is reached and grasped and the whole body thrown forward toward the horizontal.

Of two pairs of California thrashers whose nesting activities I observed, I never saw a bird approach the nest in any way but through the bush, working up from the base after coming to it on the ground. One nest was about four feet above ground in a bush, and the birds here often left in the same manner in which they had come—except when frightened off, when they flew down to the ground. Another nest was about twelve feet up in a live oak; its owners usually flew out of the tree, dropping then quickly to the ground, but, like the other pair, they never approached the nest on the wing.

California thrashers do little flying. I have seldom seen one fly as far as thirty yards. More frequently, a bird may be seen to drop down from the top of a high bush or small tree in a swooping fall, with wings outstretched, making only a few wingbeats on taking off, and again on landing. From a height of from fifteen to twenty feet the bird lands only about thirty feet away, and correspondingly closer for lesser heights.

The California thrasher is resident throughout its range.

*Toxostoma dorsale*.—I have not had the opportunity of analyzing the digging operations of the crissal thrasher, but on the few occasions when crissals have been seen digging, they were doing so in characteristic California thrasher fashion. The use of the bill may safely be said to be similar in the two species.

In their locomotion, crissal thrashers are again like the California thrasher. They prefer, likewise, dense and continuous cover, such as that afforded by mesquite thickets, to which they are almost exclusively restricted, as the California thrasher is to the chaparral. Beneath the cover of the dense mesquite they move quickly along, in and out, with long, graceful strides, head forward, tail high, stopping here and there to dig or to whisk the litter aside in search of food. They are likewise agile in scrambling about in the thorny trees, working their way up toward the tops, the favored singing posts.

Crissal thrashers, too, are little given to flight. In the field, one's most common sight of them is a sudden, brief glimpse of a bird abruptly dropping from a bushtop to the ground in a short swoop, wings outspread. Pursued, they make off rapidly on the ground, turning and twisting among the bushes, only occa-

sionally taking to wing. Sometimes one may fly for twenty to thirty yards. One of the few crissals I saw in flight is thus described in my field notes: "... its long tail held straight out behind, the head extended forward, it would make a few rapid wingbeats; then with outstretched wings, which looked ridiculously short, it would sail on, only for a few feet, then repeat."

Crissal thrashers are sedentary birds, but there is evidence of seasonal vertical movements in some populations. Mearns (1886, p. 298) reports that the species is "undoubtedly far more plentiful in the Verde Valley [Arizona] during the winter season than in summer, when many of those which winter here move upward into the zone of scrub-oaks, in which they breed in abundance. . . . The exodus takes place about the end of February after which the species becomes comparatively scarce; and by the middle of March nearly all of those remaining are settled and occupied with domestic affairs."

*Toxostoma lecontei*.—The Leconte thrasher is similar to the two species just previously discussed in the use made of the bill and in locomotion and frequency of flight.

Its digging is entirely like that of the California and the crissal thrashers. E. I. Dyer, who for more than three years has kept daily watch on the behavior of a pair of California thrashers at his home in Piedmont, California, after observing Leconte thrashers digging in the upper San Joaquin Valley in California, informed me that he was unable to distinguish their digging habits from those of the California thrasher, which he knows so intimately.

The Leconte thrasher prefers somewhat more open country than do the California and crissal thrashers, with sandy soil and scattered bush. Perhaps in correlation with its more open habitat is the fact that it may more often be seen on the wing than are the latter species.

In the upper San Joaquin Valley, near McKittrick, California, Leconte thrashers were found concentrated along deep draws and washes, where the salt-bush (*Atriplex*), characteristic of the habitat, was much more dense and more nearly continuous than on the surrounding ground. When disturbed, these birds frequently flew out of the atriplex thickets in a low circular flight which took them out in the open, then back again to the thick brush farther along the draw. In such flights the birds were usually low, very near the ground, and it was sometimes difficult to determine whether they were flying or running.

My experience with Leconte thrashers agrees almost exactly with that of Mearns (1886, pp. 304-305), who found that Lecontes "ran and hid with as much agility and cunning as the Chaparral Cock. . . . They seldom arose from the ground, and then only skimmed over the brushwood a little way, and then ran swiftly on in zig-zags, amongst the bushes and cactuses. They were secured with great trouble and exertion. . . . They always managed to retreat so adroitly whether by running among the bushes or flying close to the earth, that we were completely baffled at each attempt to shoot them. When flying they dropped low down, and performed a part of each flight in a tortuous course under cover of the sage-brush, ascending to the top of a mesquite like

a shrike. . . . Their speed when running upon the ground is truly wonderful. A pair of them were running upon the railroad, and for a little way kept ahead of our trotting horses with ease."

The Leconte thrasher is resident throughout its range.

*Summary.*—All species of *Toxostoma* do much of their foraging on the ground. The feet are not used for scratching. *Rufum* and *bendirei* peck and probe with the bill or poke around in litter, sometimes hammering the bill straight into the ground. *Curvirostre*, *redivivum*, *dorsale*, and *lecontei* all dig, that is, excavate holes, sometimes of a good size, using the bill like a pick, or as a tool with which to whisk litter from side to side. *Curvirostre* also pokes and hammers with its bill, as do *rufum* and *bendirei*; it is perhaps a less frequent and less proficient or powerful digger than is *redivivum*, *dorsale*, or *lecontei*.

All species of *Toxostoma* walk or run easily and skillfully. The tail is held low in *rufum*, *bendirei*, and *curvirostre*; it is carried up at a sharp angle in *redivivum*, *dorsale*, and *lecontei*. In *curvirostre* the gait is jerky and stiff legged; *redivivum*, *dorsale*, and *lecontei* are the swiftest and most accomplished runners.

*Rufum*, *bendirei*, and *curvirostre* make extensive use of flight in their daily activities, and often fly at heights of thirty feet or more; *redivivum*, *dorsale*, and *lecontei* seldom fly, are not skillful fliers, and are never seen very high above the low brush of their typical habitat. *Lecontei* may be seen on the wing more frequently than *redivivum* or *dorsale*, perhaps as a consequence of its more open habitat.

*Rufum* and *bendirei* undertake semiannual migrations; the others are non-migratory, though parts of populations of *dorsale*, at least in certain regions, extend or restrict their vertical range seasonally.

### BILL CURVATURE

The most striking structural peculiarity of thrashers is the curved bill characteristic of most species (fig. 2, A-J). For practical reasons, the skeletal framework of the bill—the bony upper and lower jaws—has been used for analysis. The skeletal material available is itemized on page 366.

A quantitative expression of the degree of curvature in the several species was sought in the following manner. With a Leitz macroscopic drawing apparatus, tracings were made of the lower edge of the upper jaw, from the tip back to the posterior edge of the descending process of the nasal bone. This posterior point of reference is at the anterior end of the infratemporal arch; the arch could not be included, because of its great flexibility. All tracings were made under the same magnification, about  $\times 2$ . The line so traced approximates an arc and was measured as though it were a true arc (fig. 3, arc A-B). A perpendicular (C-D) was drawn to bisect the chord of this arc; this also bisects the arc (at X). Perpendiculars were then drawn (E-E', E''-E') to bisect the chords A-X, X-B. These perpendiculars, extended, meet at the center (E') of the circle of which the arc is a part. The radii may then be drawn

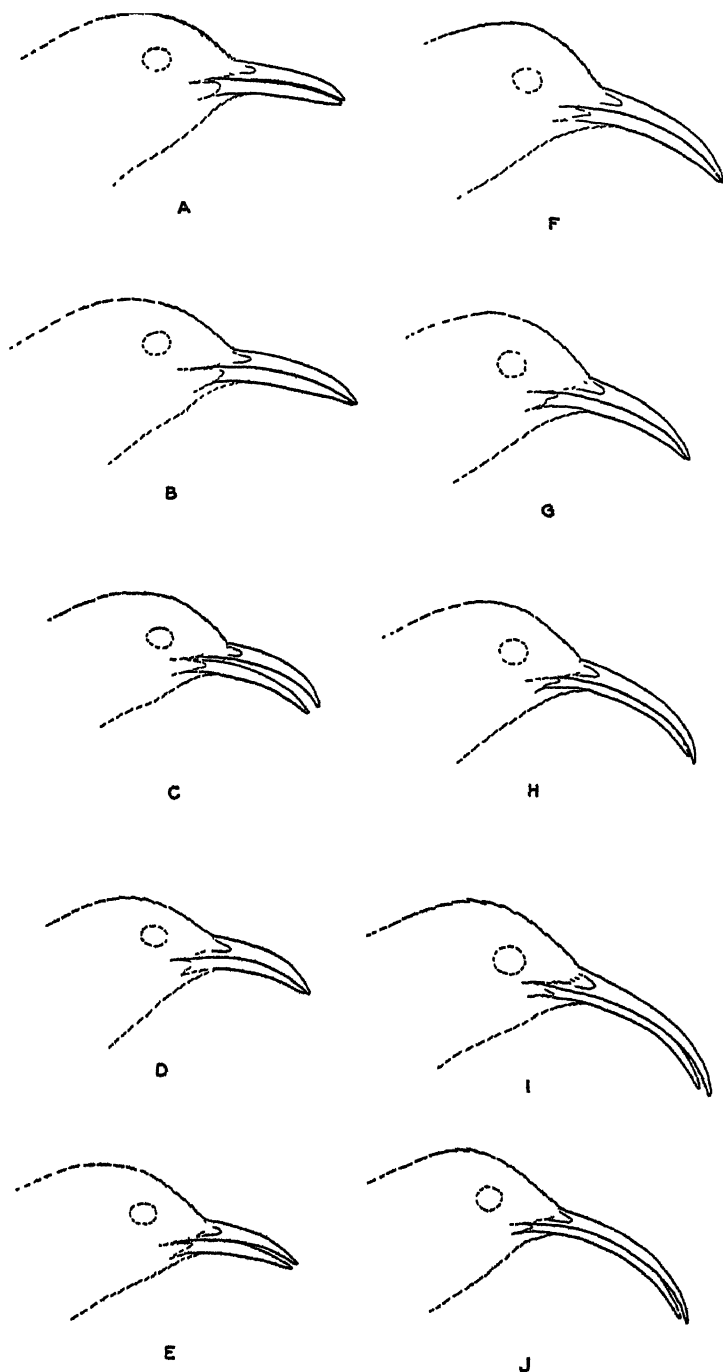


Fig. 2. Variation in length and curvature of the bill in the genus *Toxostoma*. A, *rufum*; B, *longirostre*; C, *guttatum*; D, *cinereum*; E, *bendirei*; F, *ocellatum*; G, *curvirostre*; H, *lecontei*; I, *redivivum*; J, *dorsale*. Drawings of head outlines made directly from study skins with a Leitz macroscopic drawing apparatus. Each figure somewhat more than  $\frac{2}{3}$  natural



from each end of the arc (A-E', B-E') ; the angle (Y) between these radii, read directly with a protractor, represents the degree of arc.

Three tracings were made for each individual, the degrees of arc for each were averaged, and the average for each species was determined from series of specimens. The results are given in table 1.

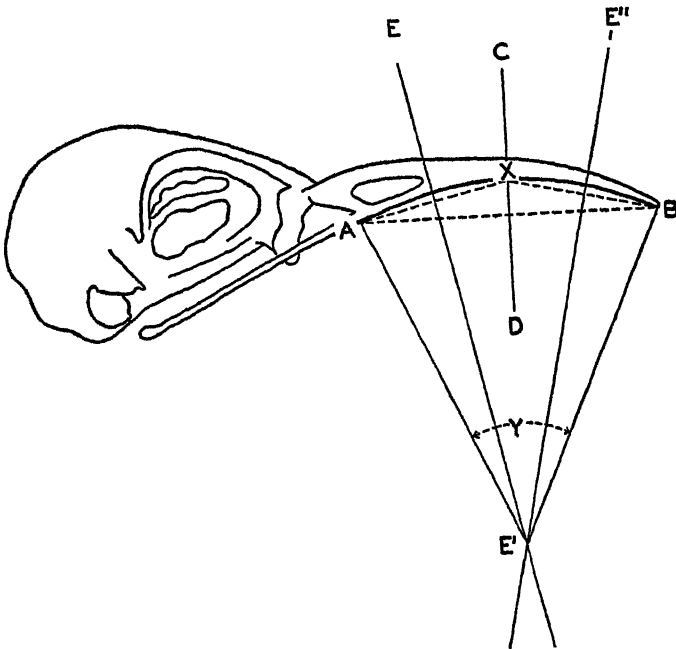


Fig. 3. Diagram to show method of measuring bill curvature. See pp. 350, 352.

As has been mentioned, the curve of the bill is not a true arc, and the figures in table 1, representing averages of the curves, therefore give only an approximate relative index for comparison of the different species. Actually, the curve

TABLE 1  
CURVATURE OF BILL IN SIX SPECIES OF THRASHERS (TOXOSTOMA)  
MEASURED IN DEGREES OF ARC

| Species                  | Number | Average | Minimum | Maximum |
|--------------------------|--------|---------|---------|---------|
| <i>rufum</i> .....       | 14     | 16-17   | 10      | 20      |
| <i>bendirei</i> .....    | 14     | 26-27   | 20      | 32      |
| <i>curvirostre</i> ..... | 27     | 34-35   | 31      | 41      |
| <i>lecontei</i> .....    | 16     | 37-38   | 33      | 44      |
| <i>redivivum</i> .....   | 14     | 41-42   | 35      | 48      |
| <i>dorsale</i> .....     | 12     | 42-43   | 37      | 48      |

is less in the proximal half of the jaw and greater in the distal half. The nature of the curve may be analyzed by measuring the arc for various segments of the bill, in the same way as was done for the whole. In *Toxostoma redivivum*, for

example, the basal half of the upper jaw approximates an arc of  $11^{\circ}$ , and the distal half, one of  $26^{\circ}$ . The practical difficulties encountered, especially in tracing accurately each point along the curve, prevented the carrying out of this kind of analysis in detail.

Because of the method used in measuring the curve, it follows, obviously, that the degree of arc will increase with increased length of bill; it is, in fact, an expression of the length of a segment of a circle. The correspondence between absolute bill length and degree of curvature among the different species is not, however, a close one; this is shown in figure 4, *a*, by differences in

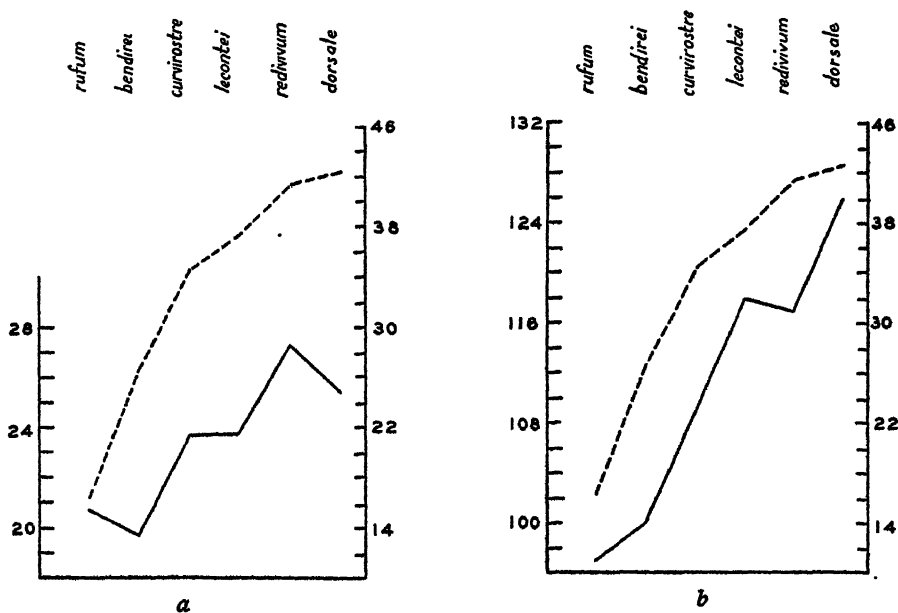


Fig. 4, *a*. Relation of absolute bill length to curvature in the genus *Toxostoma*. Solid line represents length of upper jaw, in millimeters (scale at left); broken line represents approximate curvature in degrees of arc (scale at right).

*b*. Relation of relative bill length to curvature in the genus *Toxostoma*. Solid line represents length of upper jaw as percentage of thoracic length (scale at left); broken line, as in *a*.

the direction of slope at corresponding points in the two curves. These discrepancies are resolved in large part when the degree of curvature is plotted against relative bill length, that is, length in relation to body size (fig. 4, *b*). The only deviation in the curves is caused by *redivivum*. This may be an instrumental error, since *redivivum* has the greatest absolute bill length, and there is greater chance of error because of breakage of the extremely attenuated tip of the bony jaw.

#### CHANGES IN FORM OF BILL DURING ONTOGENY

Merriam (1895, pp. 57-58) directed attention to the changes in form shown by the bill during individual development in *Toxostoma lecontei* and published figures illustrating the transition from the relatively straight bill of the young

nestling to the curved bill of the adult. For comparison, similar figures are here presented for *curvirostre* and *redivivum* (fig. 5, A-J), in which species the adults have moderately decurved bills and strongly decurved bills, respectively. The younger stages are essentially similar in the two species and similar also in the young of a straight-billed thrasher such as *rufum*. These facts are

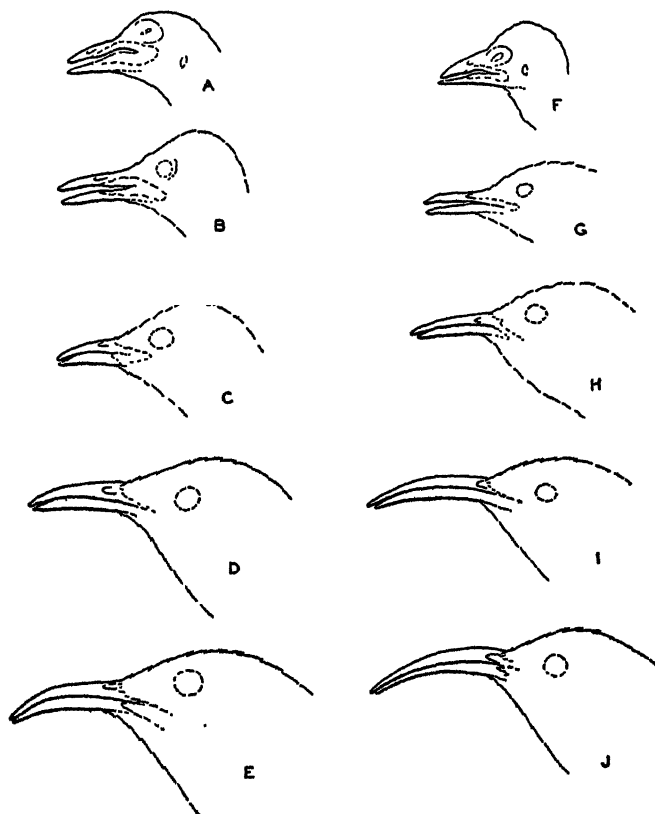


Fig. 5. Changes in form of bill in the course of development. A-E, *Toxostoma curvirostre*; F-J, *Toxostoma redivivum*. The last figure in each series represents an adult. Traced from photographs.

interpreted as emphasizing, first, that the curved bill is a specialization derived from the straight-billed type, and, second, that curvature appears coincident with a lengthening of the bill.

It may be mentioned here that the only available paleontological evidence indicates, circumstantially, that in *redivivum* the bill was markedly decurved in Pleistocene times (see p. 355).

#### OTHER STRUCTURAL FEATURES IN THE SKULL

*Mandibular symphysis.*—There is a slight but definite increase in the relative length of the symphyseal portion of the mandible accompanying increased curvature (table 2). This probably indicates that the increase in length of bill

in species where the bill is more curved results chiefly from increase in the distal, that is, the more curved part. Calculations of the relative postsymphyseal length of the mandible (table 3), though not conclusive, appear to substantiate this idea.

TABLE 2

ABSOLUTE AND RELATIVE LENGTHS OF SYMPHYSEAL PART OF MANDIBLE IN *TOXOSTOMA*

| Species                  | Number | Average length (mm.) | Percentage of total length of mandible |
|--------------------------|--------|----------------------|----------------------------------------|
| <i>rufum</i> .....       | 24     | 10.7                 | 29                                     |
| <i>bendirei</i> .....    | 16     | 10.3                 | 27                                     |
| <i>curvirostre</i> ..... | 29     | 12.8                 | 30                                     |
| <i>lecontei</i> .....    | 15     | 14.2                 | 35                                     |
| <i>redivivum</i> .....   | 16     | 16.2                 | 36                                     |
| <i>dorsale</i> .....     | 14     | 15.4                 | 37                                     |

TABLE 3

AVERAGE LENGTH OF POSTSYMPHYSEAL PART OF MANDIBLE IN *TOXOSTOMA*  
EXPRESSED IN PERCENTAGE OF THORACIC LENGTH

| Species                  | Percentage | Species                | Percentage |
|--------------------------|------------|------------------------|------------|
| <i>rufum</i> .....       | 1.22       | <i>lecontei</i> .....  | 1.33       |
| <i>bendirei</i> .....    | 1.37       | <i>redivivum</i> ..... | 1.22       |
| <i>curvirostre</i> ..... | 1.38       | <i>dorsale</i> .....   | 1.31       |

*Temporal fossa*.—The temporal fossa is bounded below by a ridge, which is projected forward from the posteroventral wall of the orbit as a process; these structures are called the *suprameatic ridge* and *suprameatic process*. The suprameatic ridge is separated below from the upper border of the auditory meatus by the *suprameatic area*.

With increased curvature of the bill, the suprameatic ridge is shifted upward, toward the postorbital process, with the result that the temporal fossa is reduced in width, with a concomitant increase in width of the suprameatic area (fig. 6, A-G). Thus, although the temporal fossa is very wide and the suprameatic area narrow in a straight-billed form like *rufum*, the temporal fossa in species with extremely curved bills, such as *redivivum*, is quite narrow, and is no wider than the suprameatic area.

A cranial fragment from the Rancho La Brea Pleistocene, with the temporal region well preserved, is indistinguishable from Recent examples of *Toxostoma redivivum* (Engels, 1935, p. 258); the position of the suprameatic ridge and consequent relative size of the temporal fossa are essentially as indicated in figure 6, F. In view of the apparent correlation between bill curvature and relative diminution of the temporal fossa now indicated, this may be taken as circumstantial evidence that the bill of *redivivum* was markedly decurved in Pleistocene times.

*Overgrowth of frontal region.*—In *rufum*, and especially in *bendirei*, there is a tendency toward a rolling over of the frontal region at the nasofrontal hinge, at the base of the bill. In neither species is it a constant character, but a majority of individuals show some evidence of this overgrowth. There is no indication of similar overgrowth in other thrashers.



Fig. 6 Camera lucida drawings of the temporal region in seven species of *Toxostoma*. Note the relative sizes of the temporal fossa and supraorbital area and the slope of the supraorbital ridge. The broken line bounding the temporal fossa posteriorly is the scar of *M. adductor mandibulae externus (superficialis)*; that behind the post-orbital process is the scar of *M. dermotemporalis*. A, *rufum*; B, *cinereum*; C, *bendirei*; D, *curvirostre*; E, *lecontei*; F, *redivivum*; G, *dorsale*.

#### CORRELATION OF BILL CURVATURE AND THE DIGGING HABIT IN *TOXOSTOMA*

From the foregoing analysis of bill curvature and the previous account of habits of thrashers, it is apparent that there is a direct correlation between the possession of a curved bill and the manifestation of the digging habit. *Rufum* and *bendirei* have relatively straight, short bills and have never been observed to dig. *Lecontei*, *redivivum*, and *dorsale* have relatively long, curved bills, and one of their most characteristic habits is digging for food. *Curvirostre*, with a bill of intermediate length and curvature, also shows ability to dig, but does so only rarely.

The only essential difference between straight pecking at the ground and digging, that is, the excavation of holes, lies in the tool employed. If the tool is straight, it disturbs only the dirt lying in its immediate path when it is hammered into the ground and withdrawn. But if a curved tool is swung into the ground with the same movement, its path of entrance describes an arc, and, when it is withdrawn, the dirt lying behind the tool, within the arc, is broken

up and dislodged. There results the kind of hole that is made by a pickax; and this is essentially the kind of hole a curve-billed thrasher digs. Given, then, the habit of hammering the bill into the ground, only slight adjustments in behavior are necessary to transform this into the digging habit, once there has been accomplished the change in the tool, that is, the development of extreme curvature, which itself comes with increased length. One of these adjustments in behavior would consist in the establishment of the pulling or hooking type of head-and-neck movement, following the downthrust of the bill by which the dirt is thrown clear. Other more subtle adjustments would be of a psychological nature, such as give the apparently intense purposefulness and planfulness to the digging, for example, of a California thrasher as it tunnels out a ground spider or a Jerusalem cricket.

The relative increase in length of the mandibular symphysis in curve-billed, digging forms is of obvious mechanical advantage in that it provides a rigid entering wedge and a firm, strong tool for breaking up the dirt lying behind it. The relative lengthening of the symphysis is probably an accompanying consequence of the increase in length of the bill upon which increased curvature is attendant; though it is not causally related to the development of the digging habit, it is of mechanical advantage in digging.

The shifting upward of the suprameatic ridge and consequent narrowing of the temporal fossa, which accompanies increased curvature, is related to changes in the external mandibular adductor muscle and is discussed in the section on musculature (pp. 358-359).

The overgrowth of bone in the nasofrontal region is reminiscent of the condition described by Burt (1930, pp. 471-472, 475) for woodpeckers, where the extent of the overgrowth is correlated with the amount of pecking done. In the thrashers it may be associated with ground pecking. Its absence in the curve-billed forms is probably to be explained by the fact that in these the force is not transmitted directly against the base of the bill at the nasofrontal hinge, because of the bill's curvature.

#### INTERGENERIC AND INTERSPECIFIC VARIATION IN THE MUSCULATURE OF THE MIMIDAE

In seeking evidence of special adaptations in the myology of thrashers, use was made of a number of alcoholic specimens, representing 12 species in 5 genera of Mimidae, as follows: *Toxostoma rufum*, *T. bendirei*, *T. curvirostre*, *T. lecontei*, *T. dorsale*, and *T. redivivum*; *Dumetella carolinensis*; *Mimus polyglottos*; *Nesomimus melanotis*, *N. macdonaldi*, and *N. parvulus*; and *Oreoscoptes montanus*. The extensive skeletal material at hand (itemized on p. 366) was also used as far as it permitted—for example, in checking individual variations in muscle depressions, scars, and processes.

Preliminary dissections usually were made on the crow (*Corvus brachyrhynchos*). For purposes of comparison with a representative of a nearly related family, some dissections were made also on the cactus wren (*Heleodytes brunneicapillus*).

The entire musculature of the California thrasher (*Toxostoma redivivum*) was carefully studied and notes were recorded on the origin, insertion, and general disposition of each muscle. With use of these notes, and of partly dissected specimens of the California thrasher, the muscles of the head, neck, limbs, and tail were directly compared among the several species of *Toxostoma* and the other species of Mimidae at hand. A complete description of the musculature will not be presented here; the myology of the group, in most details, is that typical of passerines, as described by Shufeldt (1890) for the raven (*Corvus corax*).

Shufeldt's work, it is recognized, is not without a number of confusing errors and omissions and is generally inconvenient as a ready reference. Although this situation has been rectified in part by Lakjer's description of the jaw musculature of *Corvus frugilegus*, (1926), Hudson's review of the hind-limb musculature of *Corvus brachyrhynchos* and *C. corax* (1937), and Engels' re-description of the tongue musculature in *C. corax* (1938c), a critical review of the myology of another passerine form probably would be welcomed by the student of avian morphology. Only a few of the muscles offer peculiarities pertinent to the theme of this paper, however, and I shall discuss only these muscles at this time; a complete description of the myology of the California thrasher, with critical comments on Shufeldt's "Myology of the Raven," will be presented in another paper.

The terminology here used is essentially Shufeldt's (1890) and Burt's (1930). For the jaw musculature, the names proposed by Lakjer (1926) are followed.

Generic or specific variations were found to exist with respect to *Mm. adductor mandibulae externus, pterygoidei dorsalis et ventralis, flexor capitis inferior, longus colli anterior, pectoralis pars propatagialis, latissimus dorsi* and *tensor patagii brevis*, as follows.

*M. adductor mandibulae externus*.—This is the most superficial of the muscles which act in closing the jaws. It consists of the outer portion of the heterogeneous muscle mass usually included under the term *M. temporalis*, together with the muscle bundle usually called *M. masseter*. It is crossed by the postorbitomandibular ligament and is covered by the temporal fascia. The eyeball rests against its rostral margin. Medially, it is separated from the deeper jaw muscles by the *M. bulbo-pseudotemporalis*, which runs at right angles to its fibers in a parallel plane and by the mandibular ramus of the trigeminal nerve.

Lakjer (1926) distinguishes superficial, medial, and deep portions; it is the superficial portion that is here of interest. Typically, this part arises from the lateral border and rostral surface of the suprameatic ridge, from the temporal fossa and the postorbital process, and from the caudolateral margin of the orbit, immediately above the foramen for the trigeminal nerve. It is inserted by a tough aponeurotic sheet on the dorsal margin of the mandibular ramus from the base of a tubercle above the mandibular foramen to a point slightly rostral thereto.

As has been indicated in the discussion of bill curvature, the position of

the suprameatic ridge and the consequent relative extent of the suprameatic area and the temporal fossa are specifically variable in the species of *Toxostoma* (fig. 6, A-G). This is now seen to be but an expression of the relative development of the superficial portion of the external mandibular adductor muscle. In *rufum* and *bendirei* the moderately large temporal fossa is filled with this muscle, the size of which is typical of passerines, in which the jaw musculature is neither excessively heavy nor comparatively weak. In *lecontei*, *redivivum*, and *dorsale* the muscle is relatively small, in correspondence with the narrow, shallow temporal fossa. *Curvirostre* is intermediate in this respect.

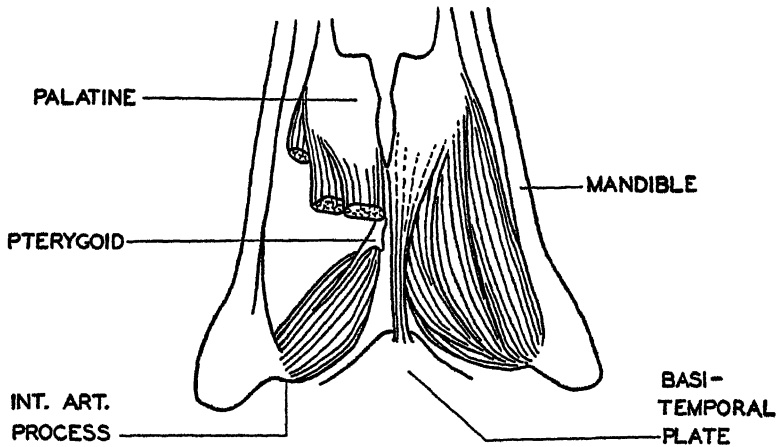


Fig. 7. *Heleodytes brunneicapillus*. Ventral view of the pterygoideus muscle complex. In the right half of the figure, the muscles are shown as they appear on removal of the mucosa of the mouth and pharynx. On the left, the retractor palatine portion of the muscle is entirely removed, and the portion arising from the palatine and inserting on the mandible is removed except at its origin.

The muscle is better developed in *lecontei* than in either *redivivum* or *dorsale*. Other mimids are like *Toxostoma rufum* and *T. bendirei*. Neither in *Toxostoma* nor in other mimids do any muscle fibers whatever arise from the suprameatic area; this area is covered directly by the integument.

*M. pterygoideus*.—This is the heaviest and strongest of the jaw muscles; it lies against the floor of the skull, in the roof of the oral and pharyngeal cavities, by the dorsal and lateral lining of which it is covered. It also forms a part of the floor of the orbit. Lakjer (1926) distinguishes a dorsal and a ventral portion, and sometimes a lateral and a medial for each of these; but I have not been able satisfactorily to separate these various parts in the passerines. The muscle arises from the posterior, widened part of the palatine, from its dorsal and ventral surfaces and lateral border, and from most of the surface of the pterygoid. The insertion is made, for the most part, on the mandible, including the summit of the articular process, its rostral face, and the adjacent part of the medial surface of the mandibular ramus; the lateralmost fibers usually extend around the ventral border of the ramus to insert on its lateral surface just below the articular area.



In passerines (Lakjer, 1926, p. 66, *Corvus*), a few of the more medial fibers have left the mandible, and insert on the lateral surface of the parasphenoidal rostrum and on the basitemporal. Moller (1930, pp. 688-689) described these fibers as the *M. retractor palatini*, and objected to consideration of them as a part of the pterygoideus; later (1931, p. 129), he reversed his stand, recognizing the homology, but maintaining the name for convenience.

In *Heleodytes*, a wren, these fibers (*M. retractor palatini* of Moller) form a very small bundle which arises from the posteroventral margin of the palatine,

medially (fig. 7). Insertion is made on a tubercle on the anterior edge of the basitemporal plate, near the mid-line. None of these fibers comes from the pterygoid, and none is visible in the floor of the orbit.

In all mimids this bundle is larger, and has a more extensive origin. In *Mimus*, it is joined by a distinct group of fibers from the dorsal surface of the pterygoid, near its medial end. This group of fibers is visible in the posteromedioventral part of the orbit. *Oreoscoptes*, *Dumetella*, and *Nesomimus* (fig. 8) are essentially similar.

In all species of *Toxostoma* this portion of the pterygoideus inserting on the basitemporal is still more extensive. In *rufum* all the fibers coming from the ventral area of the palatine, except the extreme lateral edge, are inserted on the basitemporal, and the part from the dorsal surface of the pterygoid appears heavier. In *bendirei*, a few more fibers come from the dorsal surface of the palatine, medially, and thus

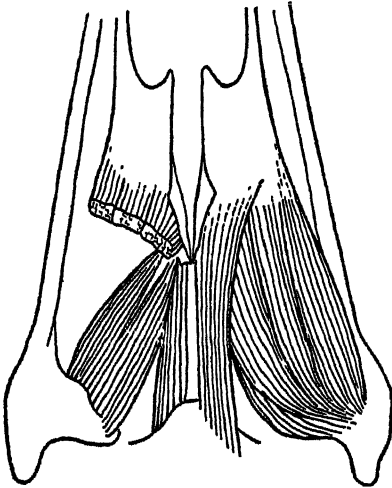


Fig. 8. *Nesomimus macdonaldi*. Ventral view of the pterygoideus muscle complex; dissection as in figure 7. Note, to the right, the relatively greater mass of the retractor palatine portion of the muscle, and, to the left, the insertion on the basitemporal plate of some of the fibers from the dorsal aspect of the pterygoid bone.

are apparent in the floor of the orbit. *Curvirostre* is similar, but the entire mass seems heavier. In *lecontei* and *dorsale* this latter portion is almost as wide and heavy as the portion running from the dorsal surface of the palatine to the mandible; in *redivivum* (fig. 9) it is much wider, the mandibular portion arising only from the lateral edge and posterolateral spine of the palatine.

To summarize: In *Heleodytes*, as probably in most passerines, the greater part of the pterygoideus muscle inserts on the mandible; a few fibers from the medial ventral angle of the palatine insert on the basitemporal. In all mimids these are joined by a bundle of fibers from the dorsal surface of the pterygoid. *Toxostoma* differs from other mimids in that all this part of the pterygoideus is heavier; almost all the fibers from the ventral surface of the palatine insert on the basitemporal. In its extreme development (*redivivum*), most of the fibers from the dorsal surface of the palatine are also included, so that that part of

the pterygoideus which inserts on the basitemporal is here almost as large as that which inserts on the mandible.

*M. flexor capitis inferior*.—This is the chief flexor of the head. It extends from the hypapophyses of the anterior cervical vertebrae to the basitemporal plate on the base of the skull; it lies on the ventral side of the anterior part of the neck, where it is the most superficial muscle, directly beneath the oesophagus. The diamond-shaped muscle mass formed by the fusion in the mid-line of the members of the pair is penetrated by the internal carotid artery, which bifurcates immediately on emerging, each branch then running obliquely forward to either ventrolateral angle of the head across the superficial face of the muscle.

In all the mimids studied, except *Toxostoma*, this muscle displays the typical passerine arrangement, taking origin by fleshy and tendinous digitations from the ventral surface of the atlas, the hypapophyses of the 2d, 3d, and 4th, and the haemapophyses of the 6th cervical vertebrae. In *Toxostoma*, however, the muscle arises also in part from the haemapophyses of the 7th cervical vertebra; in this genus it is thus longer and appears to be generally more heavy than in other mimids. This is true of all species of *Toxostoma*. The difference is to be seen at a glance, since the internal carotid artery, which emerges near the posterior end of the muscle in other mimids, appears first anterior to the middle of the muscle in *Toxostoma*.

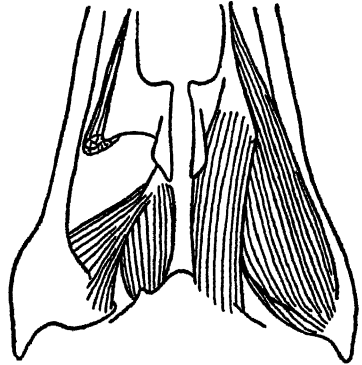


Fig. 9. *Toxostoma redivivum*. Ventral view of the pterygoideus muscle complex; dissection as in figures 7 and 8. Note that most of the fibers arising from the palatine insert on the basitemporal plate. Note also the relatively greater mass of the bundle inserting on the basitemporal plate.

*M. longus colli anterior*.—This is the chief flexor of the cervical portion of the vertebral column; it is seen as a pair of apparently band-shaped muscles on the ventral side of the middle and posterior parts of the neck; it also extends back into the anterior part of the thoracic cavity, where it forms a wedge-shaped mass on the ventral side of the vertebrae. The apparently simple muscle is in reality very complex, arising by fleshy digitations or by tendons from the haemapophyses or hypapophyses of all cervical vertebrae posterior to the 5th and from the parapophyses of the 3d to the 7th; insertions are made, usually by tendons, to the hypapophyses of the first four cervical vertebrae and to the pleurapophyses of cervical vertebrae 5–10 inclusive. By its action each vertebra anterior to the 10th is flexed on its fellow next posterior.

In *Mimus*, *Nesomimus*, *Dumetella*, and *Oreoscoptes* the posteriormost point of origin is the hypapophysis of the 15th (1st thoracic) vertebra; in *Toxostoma*, this is extended back at least to the next (2d thoracic) vertebra.

The more posterior origin of this muscle in *Toxostoma* is evident also from examination of skeletons. In *Mimus*, *Dumetella*, and *Oreoscoptes*, hypapophyses occur back only to the 1st thoracic vertebra; very infrequently there may

be a small hypapophysis on the 2d thoracic vertebra, also. But in all species of *Toxostoma* there is in all individuals a large hypapophysis on the 2d thoracic vertebra. There may also be additional hypapophyses; each species is variable in this respect, but certain tendencies can be made out.

In *rufum* and in *bendirei*, a majority of individuals have at least a small process on the 3d thoracic vertebra, occasionally quite large. In each series about 10 per cent of the individuals have two of the hypapophyses fused, those on the 1st and 2d thoracic vertebrae in *rufum*, on the 2d and 3d in *bendirei*.

In *curvirostre* almost all have a hypapophysis on the 3d thoracic vertebra, which is relatively large in about 30 per cent of the individuals. In a few the hypapophyses on the 2d and 3d vertebrae are fused.

In *lecontei* only an exceptional individual has a hypapophysis on the 3d vertebra; no fusion is to be noticed.

In *dorsale* all have at least a small bump or ridge on the 3d vertebra. In half the individuals the 2d and 3d thoracic vertebrae are fused both through their neural spines and their hypapophyses; about 20 per cent have the 4th also fused with the 2d and 3d.

Although *lecontei* and *dorsale* have similar habits and are almost exactly alike in size, *dorsale* is much more like *redivivum* than is *lecontei*, in its vertebral column. In *redivivum* all individuals have a hypapophysis on the 3d vertebra, which in most of them slopes forward and is fused with that on the 2d. The 2d and 3d thoracic vertebrae are usually fused, sometimes also the 4th.

*M. pectoralis pars propatagialis* (Gadow, 1891).—From the free ventral surface of *M. pectoralis major* two slips are given off to the tensors of the patagium; the more medial is inserted on *M. tensor patagii longus*, the more lateral on *M. tensor patagii brevis*. The slip to the *brevis* is entirely tendinous in all the mimids studied, as is that to the *longus* in *Dumetella* and *Toxostoma*. In *Mimus*, *Nesomimus*, and *Oreoscoptes*, however, the slip to the *longus* is muscular, only a short distal portion being tendinous, and the whole is about the length of the tendinous slip in *Toxostoma*, which thus represents the muscular portion plus the tendon.

*M. latissimus dorsi*.—As is usual among passerines, this muscle is divided into two parts which cross each other near their insertion, the posterior portion passing beneath the anterior one to be inserted proximal to the latter's point of insertion. In *Toxostoma redivivum* the anterior portion is ribbonlike, about 3 mm. wide throughout its length; the posterior portion is flattened, triangular, 10 mm. wide at its origin, and 2 mm. wide when it passes beneath the anterior portion, 2.5 cm. distad.

This is one of the few muscles strikingly variable within the family Mimidae; the variation concerns the relative development of the two parts. The condition just described for *Toxostoma redivivum* represents one extreme; *Oreoscoptes montanus* shows the other, in which the anterior portion is about twice the width of the posterior portion. Other species show all manner of gradation between these extremes. *Nesomimus macdonaldi*: anterior portion slightly nar-

rower than posterior; fleshy portion of posterior begins about the width of the part from its origin. In *Dumetella carolinensis* the two parts are subequal in width; fleshy part of posterior portion begins about the width of the part from its origin. *Mimus polyglottos*, *Toxostoma rufum*: like *Dumetella*. *Toxostoma bendirei*: like *T. dorsale* (see below), but posterior part less muscular, as in *T. rufum*; resembles *Nesomimus*. *T. curvirostre*: the two parts are subequal in width, as in *T. rufum*, but the cranialmost fibers of the posterior portion arise directly from the neural spine instead of from a thin sheet of connective tissue, as they do in all species previously mentioned. *T. dorsale*: anterior portion slightly narrower than posterior portion; latter arises as in *T. curvirostre*. *T. lecontei*: like *T. dorsale*, but posterior part relatively wider, more like *T. redivivum*. In all the larger species the posterior part is noticeably thicker than the very thin anterior portion.

*M. tensor patagii brevis*.—The tendon of insertion of this muscle has a peculiar and constant relation to the tendon of origin of *M. extensor metacarpi radialis longus* in all passerines, which is characteristic of that group (Garrod, 1876, pp. 508–509). The tendon of the *brevis* is attached firmly to the tendon of the extensor, but, retaining its independence after making this union, runs back to be inserted to the ectepicondyle of the humerus, near the origin of the tendon of the extensor.

In *Toxostoma*, this latter portion of the tendon of the *brevis* lies obliquely over the tendon of the extensor and is inserted *distal* to the origin of the latter tendon on the ectepicondylar prominence. This condition obtains also in all other mimids studied, with the single exception of *Oreoscoptes*, in which species the tendon of the *brevis* does not cross the tendon of the extensor and is inserted *proximal* to the origin of the latter.

#### CORRELATION OF MYOLOGICAL VARIATIONS AND PECULIARITIES OF HABIT

The differences observed with respect to the patagial portion of the pectoralis and the short tensor of the patagium do not appear to be of special or obvious significance in relation to known differences in habit. The variations in the latissimus dorsi, because of the very different direction of pull of its two parts, may have some functional significance, but I am unable to demonstrate it. The following discussion therefore treats only of the external mandibular adductor, the pterygoideus, the flexor capitis, and the longus colli anterior—four muscles the generic or specific variations of which may be looked upon possibly as adaptational in nature.

1. With respect to the superficial portion of the external mandibular adductor, the functional significance of the interspecific variations in *Toxostoma* is concerned with the angle at which the muscle pulls upon the mandible. In *rufum*, with the mouth closed or nearly closed, the fibers from the temporal fossa run very obliquely rostroventrally to the mandible, with which they form an angle of only about 30°. As a result of this low angle of pull, there is a considerable retractor component in the action of this muscle, as well as an adductor component. In an extremely specialized form such as *redivivum*,

because of the disappearance of the more caudoventral portion of the muscle, these fibers meet the mandible at an angle of more than  $45^\circ$ , when the mouth is closed or nearly so. The retractor component here is appreciably less, relative to the adductor component, than in *rufum*.

The retractor component in this muscle actually effects a slight retraction of the mandible, causing it to slide back along the quadrate. This is especially true when some object held in the bill resists the adductor action. In some birds (among passerines, notably graminivorous types) this is one phase of a "rasping" or "sawing" movement of the lower jaw, which is important in feeding.

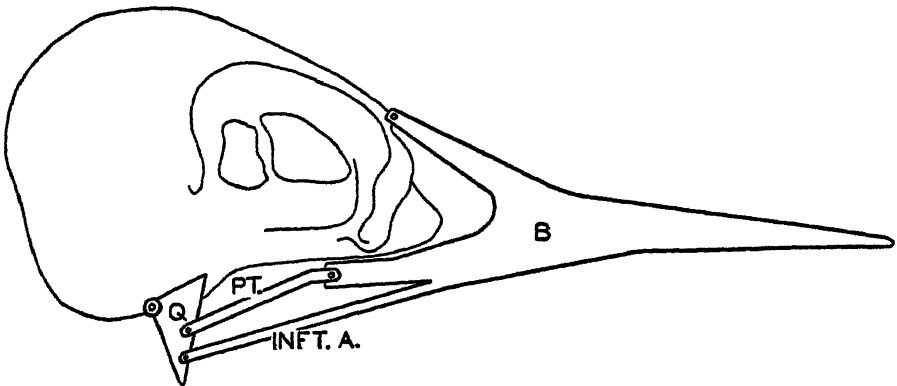


Fig. 10. Schematic representation of the lever system in the upper jaw of a passerine bird. Q, quadrate; PT., pterygoid; INFT. A., infratemporal arch; B, bony portion of upper bill (premaxillary, maxillary, nasal, and palatine).

In straight-billed forms, such a movement of the mandible does not lessen the pressure being exerted on the object held in the bill, since the mandible slides back along a line paralleling the upper jaw. Where a curved bill is concerned, however, the tip of the lower jaw lies against the upper jaw in a plane set at an angle to that in which the retraction movement progresses; retraction therefore tends to separate upper and lower jaws at their tips and to loosen the hold on an object in the tip of the beak. This is disadvantageous; it is therefore an advantage to curve-billed forms that the retraction of the lower jaw be limited. This has been accomplished in curve-billed thrashers by reducing that portion of the mandibular adductor which functions chiefly in this action. It may be recalled that the degree of reduction in this muscle is proportional to the curvature of the bill.

Finally, it seems likely that in the curve-billed forms there is little necessity for retraction of the lower jaw; this factor may be coupled with the possible disadvantages mentioned above in bringing about reduction of the retractor component of the external mandibular adductor and the associated changes in the temporal region of the skull.

2. In order to appreciate the functional significance of the specific variations in the pterygoideus muscle, outlined above, it is necessary to recall to mind the mechanics of jaw movements in birds. These have been described at various times by a number of writers, most recently by Lakjer (1926) and,

especially for passerines, by Moller (1931). Moller's is an unusually thorough and illuminating analysis. A brief description of the process as related to the movements of the upper jaw is adequate for our purpose.

The several bony elements which are involved form a lever system (fig. 10) composed of three levers: (1) the quadrate, (2) the pterygoid, and (3) the palatine plus the maxilla and other elements of the upper jaw. The infratemporal arch assists the functioning of the pterygoid in this lever system.

The protractor muscle of the pterygoid and the protractor of the quadrate, arising from the posterointernal angle of the orbit and inserting on the body of the quadrate and the quadrate head of the pterygoid, by their contraction rock the quadrate on the squamosal, throwing the anteroventral border of the quadrate forward and upward (fig. 11). The pterygoid, articulating with the

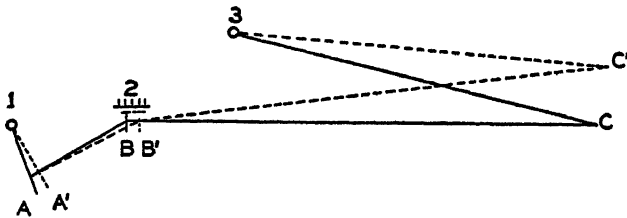


Fig. 11. Diagram to show movements in the lever system in the upper jaw of a passerine bird. When the quadrate, rocking on the quadratosquamosal articulation (1), moves forward from A to A', the pterygoid, which is prevented from moving upward by the sphenoidal rostrum (2), pushes forward against the palatine, moving from B to B'. The upper jaw, held at the nasofrontal hinge (3), is swung upward, the tip moving from C to C'.

quadrate, receives the movement and transmits it to the palatine. Here the movement is translated to a forward movement, the upward movement being hindered by the rostrum, along the under and lateral surfaces of which the pterygoid and palatine slide. At the tip of the bill the movement is again translated to an upward movement—the tip cannot move forward, as it is held by the premaxillae, nasals, and frontals behind, and therefore must move upward. The fulcrum of this lever is the nasofrontal hinge. It is to be noted that a slight movement of the quadrate becomes a rather large movement in the tip of the upper jaw.

The only muscle in passerines which acts to bring about the depression of the upper jaw is the pterygoideus, except at the very end of the movement, when the posterior adductors of the lower jaw contribute slightly to the action. Since the pterygoideus usually inserts almost entirely on the mandible, it simultaneously elevates the lower jaw. It is important to bear in mind that the muscle courses between two points, each of which enjoys considerable movement; exception is made for those fibers which Moller has called the retractor of the palatine, and which insert on the base of the skull. It is obvious that a greater degree of firmness will be given to the upper jaw through an enlargement of the "retractor palatine" portion of the pterygoideus, that is, through an increase in the number of fibers inserting on the base of the skull, rather

than on the mandible. From this consideration, it becomes obvious that the relatively tremendous increase in this part of the muscle in curve-billed forms, these being the habitual diggers, stands in direct correlation with the increased stress and strain placed on the upper bill in the digging act.

3. The flexor capitis and longus colli anterior muscles are the chief flexors of the head and neck. The more extensive origin of these muscles provides for mechanical advantages in digging, giving greater power and range to the downstrokes of the head and neck. The fusion of the thoracic vertebrae also may be looked upon as an adaptation to the digging habit, providing, as it does, a more rigid base from which the action of the neck flexor can proceed.

In conclusion, it is to be noted that those modifications in muscular mechanisms which are of obvious advantage to the curve-billed thrashers in digging occur also, in their essentials, in the straight-billed thrashers (flexors of head and neck), and even in other mimids (pterygoideus). In all species of *Toxostoma* the flexors of the head and neck extend back over at least one vertebra more than in other mimids; in all mimids, some of the fibers of the pterygoideus coming from the pterygoid bone join those coming from the palatine, which insert on the basitemporal. These basic modifications cannot in any sense be said to be primary adaptations to the digging habit. They may have been adaptive in their origin, in a remote ancestral group, in association with a habit fundamentally related to the digging habit, such as the ground pecking of straight-billed thrashers. Whatever the cause of the first appearance of these essential modifications, they provided a fundamental mechanism which enabled the thrashers to become diggers after the digging tool (the curved bill) was evolved. In other words, peculiarities of musculature common to all thrashers "pre-adapt" them to the digging habit. The specialization of the curve-billed thrashers consisted chiefly in the evolution of a curved bill, which permitted them to dig, and in the accompanying elaboration of an inherited muscular mechanism.

#### PROPORTIONS OF LIMB SEGMENTS

The material on which this phase of the study of adaptations in the thrashers is based consists of 209 skeletons of adult birds, representing 6 genera and 12 species of the family Mimidae, as follows:

|                              |    |                                       |    |
|------------------------------|----|---------------------------------------|----|
| <i>Toxostoma rufum</i> ..... | 29 | <i>Toxostoma redivivum</i> .....      | 16 |
| <i>cinereum</i> .....        | 2  | <i>Melanoptila glabirostris</i> ..... | 1  |
| <i>bendirei</i> .....        | 23 | <i>Dumetella carolinensis</i> .....   | 25 |
| <i>curvirostre</i> .....     | 39 | <i>Mimus polyglottos</i> .....        | 20 |
| <i>lecontei</i> .....        | 15 | <i>Oreoscoptes montanus</i> .....     | 23 |
| <i>dorsale</i> .....         | 15 | <i>Margarops fuscatus</i> .....       | 1  |

*Measurements.*—All measurements were made with dial-type calipers and were read to the nearest 0.1 millimeter. Measurements of the length of the following skeletal elements were recorded (tables 4 and 5): humerus, radius, ulna, carpometacarpus, phalanges 1 and 2 of digit II, femur, tibiotarsus, tarsometatarsus, and middle toe. The measurements were taken between proximal

and distal articulating surfaces in such a way that their sums would most closely approximate total limb lengths. Two linear measurements of the axial skeleton were recorded also; these were designated, arbitrarily, trunk length and thoracic length (table 6).

Hand length was taken as the sum of the lengths of the carpometacarpus, phalanx 1 and phalanx 2 of digit II (table 7). The small size of these elements, particularly of the second phalanx, appreciably increases the instrumental error in its percentage value. The adding of their separate lengths to give a single value, hand length, admits the danger of cumulative error, although there is also possibility of cancellation of errors. The fact that almost all the skeletons were disarticulated made it inconvenient to obtain the hand-length measurement directly; furthermore, the individual measurements were necessary in order to determine changes in proportion within the hand. The results obtained indicate that this method of measuring hand length was satisfactory for the purpose for which it was intended.

Wing length was taken as the sum of the lengths of the humerus, ulna, and hand (table 7). Length of the radius was used as a check against length of ulna in determining the relative length of the forearm. Of the wing-segment measurements, length of humerus is the least subject to instrumental error.

Leg length was taken as the sum of the femur, tibiotarsus, tarsometatarsus, and middle toe (table 7). In obtaining the middle-toe length, the four phalanges were cemented to a glass slide and the measurement was made from the proximal articulating surface of the basal phalanx to the tip of the ungual phalanx. The tip of this phalanx is attenuated and extremely delicate; accurate measurement was therefore difficult, and less reliance can be placed on this measurement than on other measurements of the leg segments. Of these others the most dependable is the length of the femur.

It was found desirable to have some linear measurement outside of the limbs to which the limb segments might be compared. Since the trunk length is probably less subject to change than any other part, its use was decided upon (table 6). The measurement, made with a flexible steel tape and read to the nearest millimeter, was taken along the middorsal line from the level of a plane passing through the two acetabulae, perpendicular to the vertebral column, to the anterior end of the neural spine of the last vertebra bearing a free rib (14th, or last cervical, vertebra). This approximates the "Rumpflänge" used by Böker (1927, pp. 312-313) for the same purpose; it is perhaps from 5 to 10 per cent shorter than Böker's. At least one of the points of reference, the anterior, can be determined more precisely than either of Böker's, but the measurement is still a relatively gross one.

As a check, a second measurement was made, the thoracic length (table 6). This was made with a dial-type caliper and was taken between the anterior articulating surface of the centrum of the 14th (last cervical) and the posterior articulating surface of the centrum of the 19th (last free thoracic) vertebra, in the mid-line. Results obtained through the use of this measurement were in essential agreement with those obtained through use of trunk-length



measurements; it was usually more convenient to use the latter measurement, since it is considerably larger.

*Ratios.*—The problem of determining proportions of limb segments in birds is attended with certain difficulties, which previous workers have not always escaped.

Larson (1930), in a study of the California road-runner, determined the ratios existing between the corresponding segments in wing and leg; and because the ratios were progressively higher as the reckoning proceeded farther and farther distally, she concluded that in the evolution of this bird "the increase in size in the leg and the reduction in the wing have occurred mostly in the distal segments" (p. 416). It may be pointed out that the data permit only of a more limited interpretation, namely, that the changes which had occurred, whatever these may have been, were most marked between the distal segments of the two limbs. The idea that there had occurred a reduction of the wing together with increase in length of leg is based on the comparison of ratios of ulna to tibiotarsus in several related genera, from which it is concluded that the road-runner "has by far the largest leg in comparison with size of wing that is found in any known cuckoo" (*op. cit.*, p. 414). As to relative size of limbs, this conclusion is justifiable, but the data presented do not demonstrate that the differences in the ratios result from evolution in opposed directions in the two limbs. The same sort of ratio might be the result of increased length of leg without wing reduction, or even the result of relatively greater increase in length of leg when both limbs are elongating.

Marples (1930), in a preliminary report of studies on the proportions of birds' wings and their changes in development, expressed the lengths of upper arm, forearm, and hand as percentages of the total wing, that is, as percentages of their sum. This method sets up serious difficulties in the way of interpretation, which cannot be overcome except by the use of other methods (see also p. 369). That is, in considering two elements as percentages of their sum, a change in the relative percentages of the two might be the result of any one of four events: increase in the first without change in the second, decrease in the second without change in the first, relatively greater increase in the first when both are increasing, or relatively greater decrease in the second when both are decreasing; and inspection of the change in percentage would not reveal which of the four events had taken place. When three elements are involved, such as the three segments of the wing, the situation is even more complicated.

I do not imply that such data are without significance; such percentages express in one way the proportions of the several segments within a limb, and these proportions must be significant in the functional mechanism. But other means of analysis are necessary to show the probable direction of the changes of which those proportions are the result.

It is true that in the particular case dealt with by Marples—changes in proportion in the course of individual development—all parts are increasing in length, although hardly at the same rate. But changes in the proportions be-

tween limb-segment lengths and general body size are also occurring, and, as is evident from the work of Böker (1927), these have significance with respect to problems which Marples saw but could not solve.

These papers by Larson and by Marples were preceded by a more comprehensive one of prime importance, Böker's study on the correlation of wing-segment proportions and type of flight (Böker, 1927). By making use of a trunk-length measurement and computing the limb-segment length : trunk length ratios, Böker was able to construct graphs which illustrated, simultaneously, the length of each segment of each limb in relation to the trunk length, and thus also in relation to one another. The latter relation, however, can be estimated only, and though this was sufficient for his purpose of comparing birds of very different habits and remote relationship, it lacks the precision necessary for ascertaining and interpreting the slight differences in proportions which one might expect to find within the limits of a genus, or even of a family.

I have tried to avoid these difficulties by calculating ratios of several kinds and analyzing the results by balancing them against one another. The ratios used are of three principal types: intramembral, intermembral and limb : trunk ratios.

For the wing, the lengths of the radius, ulna, and hand were each determined in terms of percentage of length of humerus; for the leg, the lengths of the tibiotarsus, tarsometatarsus, and middle toe were each calculated in terms of percentage of length of femur. These six intramembral ratios serve the purpose of illustrating differences in proportion among the species within each limb.

The lengths of each of the three chief segments of the wing (humerus, ulna, and hand), of each of the four segments of the leg, the total wing length, and the total leg length were expressed in terms of percentage of trunk length. Moreover, the lengths of the femur, humerus, and each of the three hand segments (metacarpus, phalanx 1 and phalanx 2 of digit II) were calculated as percentages of the thoracic length. These fourteen limb : trunk ratios illustrate specific differences in the relative length of each limb segment independently of the other segments and serve as the basis for the interpretation of the intramembral and intermembral ratios.

Five intermembral ratios were calculated, as follows: total wing : total leg; humerus : femur; ulna : tibiotarsus; carpometacarpus : tarsometatarsus; and hand phalanges : middle toe; the length of the wing segment was expressed, each time, as percentage of the length of the corresponding segment in the leg. These ratios give precise indices of specific differences in the length of one limb in relation to the other.

Any such ratios as just described may be calculated for a species in two ways: the absolute linear measurements of a number of individuals may be averaged, and ratios determined on the basis of average measurements; or, the several ratios may be determined for each individual in the series, and the average of the ratios then determined. As a result of the first method, one

obtains the proportions of an "individual" which is average for all measurements (probably no such individual exists); on the basis of the second method, one obtains the average proportions of many individuals—and these, it would seem, should more nearly represent the real values.

Use of the first method, that of calculating proportions on average measurements, rests necessarily on the assumption that the several parts to be compared vary dependently. This assumption was tested on other material and has been reported on elsewhere (Engels, 1938a). Dependent variation was demonstrated to a high but not absolute degree. However, it was found that for this material there was no appreciable difference in the results of the two methods of treatment; therefore, for the smaller series, all ratios were calculated on the basis of average measurements. Certain ratios were determined for each individual in the larger series, for the purpose of ascertaining their range of variability (tables 8 to 11) and demonstrating the reliability of the simpler method.

In either method, a weakness in the treatment, inherent in the material, must be recognized. In relatively few of the skeletons could all twelve of the desired measurements be made; many bones were shattered by shot in the collecting of the specimens, and, in many individuals, one or another of the smaller elements, especially the second phalanx of the hand, apparently had been lost. As a result, the several average measurements, or average ratios, of a given species are made each from a slightly different sample of varying size, a number somewhat less than the total number of specimens available for the species.

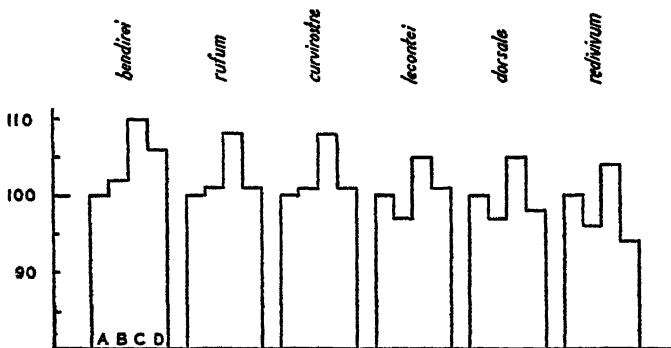


Fig. 12. Histograms illustrating intramembral ratios of the wing in *Toxostoma*. Length of each segment is shown as percentage of length of humerus. A, humerus; B, radius; C, ulna; D, manus. The species are arranged, from left to right, on the basis of decreasing relative length of the distal segments. (For data on variability in these ratios, see table 8.)

#### PROPORTIONS OF WING SEGMENTS IN *TOXOSTOMA*

Inspection of intramembral ratios for six species of *Toxostoma* reveals that when the species are arranged in the order of decrease in each ratio they stand in the series: *bendirei*, *rufum*, *curvirostre*, *lecontei*, *dorsale*, and *redivivum* (fig. 12). The difference between the extremes, *bendirei* and *redivivum*, is con-

TABLE 4  
LENGTH, IN MILLIMETERS, OF WING BONES IN SOME SPECIES OF MIMIDS

| Species                                 | Humerus |           |                    |                |                     |
|-----------------------------------------|---------|-----------|--------------------|----------------|---------------------|
|                                         | No.     | Mean      | Standard deviation | Coeff. of var. |                     |
| <i>Dumetella carolinensis</i> . . . . . | 24      | 21.7±0.08 | 0.40±0.06          | 1.84           |                     |
| <i>Mimus polyglottos</i> . . . . .      | 19      | 26.1±0.16 | 0.71±0.12          | 2.72           |                     |
| <i>Oreoscoptes montanus</i> . . . . .   | 23      | 23.4±0.10 | 0.46±0.07          | 1.96           |                     |
| <i>Toxostoma rufum</i> . . . . .        | 28      | 27.0±0.12 | 0.65±0.09          | 2.41           |                     |
| <i>Toxostoma bendirei</i> . . . . .     | 23      | 26.7±0.14 | 0.66±0.10          | 2.47           |                     |
| <i>Toxostoma curvirostre</i> . . . . .  | 38      | 28.1±0.11 | 0.66±0.08          | 2.35           |                     |
|                                         |         | Average   | Maximum            | Minimum        | Range<br>(per cent) |
| <i>Toxostoma lecontei</i> . . . . .     | 15      | 25.3      | 26.0               | 24.0           | 7.9                 |
| <i>Toxostoma redivivum</i> . . . . .    | 16      | 27.8      | 28.9               | 26.7           | 7.9                 |
| <i>Toxostoma dorsale</i> . . . . .      | 15      | 25.4      | 26.5               | 24.3           | 8.6                 |

| Species                                 | Radius |           |                    |                |                     |
|-----------------------------------------|--------|-----------|--------------------|----------------|---------------------|
|                                         | No.    | Mean      | Standard deviation | Coeff. of var. |                     |
| <i>Dumetella carolinensis</i> . . . . . | 25     | 23.0±0.12 | 0.60±0.08          | 2.60           |                     |
| <i>Mimus polyglottos</i> . . . . .      | 19     | 29.1±0.19 | 0.83±0.13          | 2.85           |                     |
| <i>Oreoscoptes montanus</i> . . . . .   | 22     | 25.2±0.14 | 0.64±0.10          | 2.53           |                     |
| <i>Toxostoma rufum</i> . . . . .        | 28     | 27.2±0.14 | 0.73±0.10          | 2.68           |                     |
| <i>Toxostoma bendirei</i> . . . . .     | 23     | 27.3±0.18 | 0.85±0.13          | 3.11           |                     |
| <i>Toxostoma curvirostre</i> . . . . .  | 38     | 28.3±0.12 | 0.75±0.09          | 2.65           |                     |
|                                         |        | Average   | Maximum            | Minimum        | Range<br>(per cent) |
| <i>Toxostoma lecontei</i> . . . . .     | 14     | 24.5      | 25.5               | 22.6           | 11.8                |
| <i>Toxostoma redivivum</i> . . . . .    | 16     | 26.8      | 28.1               | 25.0           | 11.5                |
| <i>Toxostoma dorsale</i> . . . . .      | 15     | 24.7      | 26.3               | 23.5           | 11.3                |

| Species                                 | Ulna |           |                    |                |                     |
|-----------------------------------------|------|-----------|--------------------|----------------|---------------------|
|                                         | No.  | Mean      | Standard deviation | Coeff. of var. |                     |
| <i>Dumetella carolinensis</i> . . . . . | 24   | 24.7±0.13 | 0.62±0.09          | 2.51           |                     |
| <i>Mimus polyglottos</i> . . . . .      | 19   | 31.1±0.22 | 0.95±0.15          | 3.05           |                     |
| <i>Oreoscoptes montanus</i> . . . . .   | 23   | 27.0±0.13 | 0.63±0.09          | 2.33           |                     |
| <i>Toxostoma rufum</i> . . . . .        | 26   | 29.2±0.16 | 0.82±0.11          | 2.81           |                     |
| <i>Toxostoma bendirei</i> . . . . .     | 21   | 29.3±0.20 | 0.90±0.14          | 3.07           |                     |
| <i>Toxostoma curvirostre</i> . . . . .  | 38   | 30.4±0.12 | 0.73±0.08          | 2.40           |                     |
|                                         |      | Average   | Maximum            | Minimum        | Range<br>(per cent) |
| <i>Toxostoma lecontei</i> . . . . .     | 15   | 26.5      | 27.5               | 24.7           | 10.5                |
| <i>Toxostoma redivivum</i> . . . . .    | 16   | 28.9      | 30.1               | 27.3           | 9.7                 |
| <i>Toxostoma dorsale</i> . . . . .      | 15   | 26.6      | 28.0               | 25.1           | 10.8                |

TABLE 4—(Continued)

| Species                             | Metacarpus |           |                    |         |                  |
|-------------------------------------|------------|-----------|--------------------|---------|------------------|
|                                     | No.        | Mean      | Standard deviation |         | Coeff. of var.   |
| <i>Dumetella carolinensis</i> ..... | 24         | 13.0±0.06 | 0.30±0.04          |         | 2.30             |
| <i>Mimus polyglottos</i> .....      | 20         | 16.3±0.13 | 0.56±0.09          |         | 3.43             |
| <i>Oreoscoptes montanus</i> .....   | 23         | 15.0±0.08 | 0.37±0.05          |         | 2.46             |
| <i>Toxostoma rufum</i> .....        | 29         | 15.7±0.08 | 0.45±0.06          |         | 2.87             |
| <i>Toxostoma bendirei</i> .....     | 22         | 16.0±0.11 | 0.05±0.08          |         | 3.13             |
| <i>Toxostoma curvirostre</i> .....  | 39         | 16.3±0.06 | 0.39±0.04          |         | 2.39             |
|                                     |            | Average   | Maximum            | Minimum | Range (per cent) |
|                                     |            |           |                    |         |                  |
| <i>Toxostoma lecontei</i> .....     | 14         | 14.5      | 15.0               | 13.8    | 8.3              |
| <i>Toxostoma redivivum</i> .....    | 16         | 15.1      | 15.8               | 14.5    | 8.6              |
| <i>Toxostoma dorsale</i> .....      | 15         | 14.2      | 15.0               | 13.8    | 8.4              |

| Species                             | Phalanx 1, digit II |         |         |         |                  |
|-------------------------------------|---------------------|---------|---------|---------|------------------|
|                                     | No.                 | Average | Maximum | Minimum | Range (per cent) |
| <i>Dumetella carolinensis</i> ..... | 24                  | 6.4     | 6.7     | 6.1     | 8.9              |
| <i>Mimus polyglottos</i> .....      | 20                  | 8.0     | 8.4     | 7.4     | 12.5             |
| <i>Oreoscoptes montanus</i> .....   | 23                  | 7.3     | 7.9     | 6.9     | 13.7             |
| <i>Toxostoma rufum</i> .....        | 29                  | 7.4     | 7.9     | 6.9     | 13.5             |
| <i>Toxostoma bendirei</i> .....     | 23                  | 7.7     | 8.2     | 6.7     | 19.5             |
| <i>Toxostoma curvirostre</i> .....  | 39                  | 7.5     | 8.0     | 6.7     | 17.3             |
| <i>Toxostoma lecontei</i> .....     | 13                  | 6.8     | 7.0     | 6.4     | 8.8              |
| <i>Toxostoma redivivum</i> .....    | 16                  | 6.8     | 7.2     | 6.5     | 10.3             |
| <i>Toxostoma dorsale</i> .....      | 15                  | 6.7     | 7.2     | 6.4     | 11.9             |

| Species                             | Phalanx 2, digit II |         |         |         |                  |
|-------------------------------------|---------------------|---------|---------|---------|------------------|
|                                     | No.                 | Average | Maximum | Minimum | Range (per cent) |
| <i>Dumetella carolinensis</i> ..... | 19                  | 3.7     | 4.1     | 3.4     | 8.1              |
| <i>Mimus polyglottos</i> .....      | 20                  | 4.5     | 5.0     | 4.1     | 20.0             |
| <i>Oreoscoptes montanus</i> .....   | 20                  | 4.0     | 4.3     | 3.7     | 15.0             |
| <i>Toxostoma rufum</i> .....        | 22                  | 4.3     | 4.6     | 4.0     | 13.9             |
| <i>Toxostoma bendirei</i> .....     | 23                  | 4.6     | 5.0     | 4.1     | 19.5             |
| <i>Toxostoma curvirostre</i> .....  | 34                  | 4.7     | 5.5     | 4.4     | 23.4             |
| <i>Toxostoma lecontei</i> .....     | 12                  | 4.2     | 4.4     | 3.9     | 11.6             |
| <i>Toxostoma redivivum</i> .....    | 14                  | 4.1     | 4.5     | 3.8     | 17.1             |
| <i>Toxostoma dorsale</i> .....      | 13                  | 4.1     | 4.4     | 3.9     | 12.2             |

TABLE 5  
LENGTH, IN MILLIMETERS, OF LEG BONES IN SOME SPECIES OF MIMIDS

| Species                             | Femur |           |                    |                |                  |
|-------------------------------------|-------|-----------|--------------------|----------------|------------------|
|                                     | No.   | Mean      | Standard deviation | Coeff. of var. |                  |
| <i>Dumetella carolinensis</i> ..... | 25    | 22.3±0.08 | 0.38±0.05          | 1.70           |                  |
| <i>Mimus polyglottos</i> .....      | 19    | 24.1±0.12 | 0.53±0.09          | 2.19           |                  |
| <i>Oreoscoptes montanus</i> .....   | 22    | 23.6±0.10 | 0.47±0.07          | 1.99           |                  |
| <i>Toxostoma rufum</i> .....        | 28    | 28.1±0.12 | 0.61±0.08          | 2.17           |                  |
| <i>Toxostoma bendirei</i> .....     | 21    | 26.2±0.18 | 0.83±0.13          | 3.17           |                  |
| <i>Toxostoma curvirostre</i> .....  | 37    | 28.5±0.10 | 0.58±0.07          | 2.03           |                  |
|                                     |       | Average   | Maximum            | Minimum        | Range (per cent) |
| <i>Toxostoma lecontei</i> .....     | 15    | 27.4      | 28.0               | 26.3           | 6.2              |
| <i>Toxostoma redivivum</i> .....    | 16    | 32.0      | 33.5               | 30.1           | 10.6             |
| <i>Toxostoma dorsale</i> .....      | 14    | 27.8      | 28.8               | 26.2           | 9.5              |

| Species                             | Tibiotarsus |           |                    |                |                  |
|-------------------------------------|-------------|-----------|--------------------|----------------|------------------|
|                                     | No.         | Mean      | Standard deviation | Coeff. of var. |                  |
| <i>Dumetella carolinensis</i> ..... | 20          | 37.9±0.16 | 0.70±0.11          | 1.84           |                  |
| <i>Mimus polyglottos</i> .....      | 18          | 43.4±0.21 | 0.89±0.15          | 2.05           |                  |
| <i>Oreoscoptes montanus</i> .....   | 21          | 41.2±0.22 | 1.02±0.16          | 2.47           |                  |
| <i>Toxostoma rufum</i> .....        | 25          | 46.6±0.22 | 1.11±0.16          | 2.38           |                  |
| <i>Toxostoma bendirei</i> .....     | 21          | 44.5±0.31 | 1.40±0.22          | 3.14           |                  |
| <i>Toxostoma curvirostre</i> .....  | 36          | 45.6±0.17 | 0.99±0.12          | 2.17           |                  |
|                                     |             | Average   | Maximum            | Minimum        | Range (per cent) |
| <i>Toxostoma lecontei</i> .....     | 15          | 44.6      | 45.9               | 42.9           | 6.7              |
| <i>Toxostoma redivivum</i> .....    | 14          | 52.5      | 54.6               | 50.1           | 8.5              |
| <i>Toxostoma dorsale</i> .....      | 14          | 44.4      | 46.8               | 42.7           | 9.2              |

| Species                             | Tarsometatarsus |           |                    |                |                  |
|-------------------------------------|-----------------|-----------|--------------------|----------------|------------------|
|                                     | No.             | Mean      | Standard deviation | Coeff. of var. |                  |
| <i>Dumetella carolinensis</i> ..... | 24              | 27.4±0.13 | 0.66±0.10          | 2.40           |                  |
| <i>Mimus polyglottos</i> .....      | 19              | 32.7±0.19 | 0.84±0.14          | 2.56           |                  |
| <i>Oreoscoptes montanus</i> .....   | 22              | 30.3±0.20 | 0.93±0.14          | 3.06           |                  |
| <i>Toxostoma rufum</i> .....        | 28              | 33.6±0.14 | 0.73±0.10          | 2.17           |                  |
| <i>Toxostoma bendirei</i> .....     | 21              | 33.1±0.24 | 1.09±0.17          | 3.29           |                  |
| <i>Toxostoma curvirostre</i> .....  | 38              | 32.7±0.15 | 0.90±0.10          | 2.75           |                  |
|                                     |                 | Average   | Maximum            | Minimum        | Range (per cent) |
| <i>Toxostoma lecontei</i> .....     | 15              | 31.0      | 32.1               | 29.5           | 8.4              |
| <i>Toxostoma redivivum</i> .....    | 15              | 38.4      | 39.9               | 36.5           | 8.9              |
| <i>Toxostoma dorsale</i> .....      | 13              | 32.5      | 34.5               | 31.0           | 9.4              |

TABLE 5—(Continued)

| Species                                 | Middle toe |           |                    |                |                     |
|-----------------------------------------|------------|-----------|--------------------|----------------|---------------------|
|                                         | No.        | Mean      | Standard deviation | Coeff. of var. |                     |
| <i>Dumetella carolinensis</i> . . . . . | 22         | 22.5±0.14 | 0.68±0.10          | 3.02           |                     |
| <i>Mimus polyglottos</i> . . . . .      | 20         | 25.0±0.20 | 0.89±0.14          | 3.56           |                     |
| <i>Oreoscoptes montanus</i> . . . . .   | 18         | 21.0±0.12 | 0.52±0.09          | 2.47           |                     |
| <i>Toxostoma rufum</i> . . . . .        | 24         | 27.9±0.14 | 0.71±0.10          | 2.54           |                     |
| <i>Toxostoma bendirei</i> . . . . .     | 23         | 27.4±0.19 | 0.92±0.14          | 3.36           |                     |
| <i>Toxostoma curvirostre</i> . . . . .  | 38         | 29.2±0.15 | 0.90±0.10          | 3.08           |                     |
|                                         |            | Average   | Maximum            | Minimum        | Range<br>(per cent) |
| <i>Toxostoma lecontei</i> . . . . .     | 14         | 26.2      | 27.2               | 25.3           | 7.3                 |
| <i>Toxostoma redivivum</i> . . . . .    | 16         | 31.3      | 32.8               | 30.0           | 8.9                 |
| <i>Toxostoma dorsale</i> . . . . .      | 14         | 27.3      | 28.8               | 25.5           | 12.1                |

TABLE 6

AVERAGE TRUNK LENGTH AND THORACIC LENGTH, IN MILLIMETERS, IN SOME SPECIES OF MIMIDS

| Species                             | Thoracic length | Trunk length |
|-------------------------------------|-----------------|--------------|
| <i>Dumetella carolinensis</i> ..... | 17.2            | 29.2         |
| <i>Mimus polyglottos</i> .....      | 20.0            | 32.6         |
| <i>Oreoscoptes montanus</i> .....   | 18.8            | 29.0         |
| <i>Toxostoma rufum</i> .....        | 21.4            | 36.2         |
| <i>Toxostoma bendirei</i> .....     | 19.8            | 34.2         |
| <i>Toxostoma curvirostre</i> .....  | 21.8            | 36.8         |
| <i>Toxostoma lecontei</i> .....     | 20.1            | 34.9         |
| <i>Toxostoma redivivum</i> .....    | 23.4            | 40.9         |
| <i>Toxostoma dorsale</i> .....      | 20.2            | 34.8         |

TABLE 7

TOTAL HAND LENGTH, TOTAL WING LENGTH, AND TOTAL LEG LENGTH, IN MILLIMETERS, IN SOME SPECIES OF MIMIDS

| Species                             | Hand | Wing | Leg   |
|-------------------------------------|------|------|-------|
| <i>Dumetella carolinensis</i> ..... | 23.1 | 69.5 | 110.1 |
| <i>Mimus polyglottos</i> .....      | 28.8 | 86.0 | 125.2 |
| <i>Oreoscoptes montanus</i> .....   | 26.3 | 76.7 | 116.1 |
| <i>Toxostoma rufum</i> .....        | 27.4 | 83.6 | 136.2 |
| <i>Toxostoma bendirei</i> .....     | 28.3 | 84.3 | 132.2 |
| <i>Toxostoma curvirostre</i> .....  | 28.5 | 87.0 | 136.0 |
| <i>Toxostoma lecontei</i> .....     | 25.5 | 77.3 | 129.2 |
| <i>Toxostoma redivivum</i> .....    | 26.0 | 82.7 | 154.2 |
| <i>Toxostoma dorsale</i> .....      | 25.0 | 77.0 | 131.6 |

TABLE 8

VARIABILITY IN THE INTRAMEMBRAL RATIOS OF THE WING IN THREE SPECIES OF TOXOSTOMA  
(Figures represent percentage of humerus)

| Species                            | Radius |            |                    |                |
|------------------------------------|--------|------------|--------------------|----------------|
|                                    | No.    | Mean       | Standard deviation | Coeff. of var. |
| <i>Toxostoma rufum</i> .....       | 27     | 100.7±0.31 | 1.60±0.22          | 1.59           |
| <i>Toxostoma bendirei</i> .....    | 23     | 102.5±0.29 | 1.40±0.21          | 1.37           |
| <i>Toxostoma curvirostre</i> ..... | 38     | 100.7±0.20 | 1.25±0.14          | 1.24           |
| Ulna                               |        |            |                    |                |
| <i>Toxostoma rufum</i> .....       | 25     | 108.4±0.31 | 1.56±0.22          | 1.44           |
| <i>Toxostoma bendirei</i> .....    | 21     | 110.0±0.30 | 1.39±0.21          | 1.26           |
| <i>Toxostoma curvirostre</i> ..... | 37     | 108.5±0.22 | 1.33±0.15          | 1.23           |
| Manus                              |        |            |                    |                |
| <i>Toxostoma rufum</i> .....       | 22     | 101.6±0.36 | 1.68±0.25          | 1.65           |
| <i>Toxostoma bendirei</i> .....    | 22     | 106.0±0.37 | 1.72±0.26          | 1.62           |
| <i>Toxostoma curvirostre</i> ..... | 33     | 101.3±0.39 | 2.21±0.27          | 2.18           |

TABLE 9

VARIABILITY IN THE INTRAMEMBRAL RATIOS OF THE LEG IN THREE SPECIES OF TOXOSTOMA  
(Figures represent percentage of femur)

| Species                            | Tibiotarsus |            |                    |                |
|------------------------------------|-------------|------------|--------------------|----------------|
|                                    | No.         | Mean       | Standard deviation | Coeff. of var. |
| <i>Toxostoma rufum</i> .....       | 23          | 165.9±0.52 | 2.48±0.37          | 1.49           |
| <i>Toxostoma bendirei</i> .....    | 20          | 169.8±0.76 | 3.41±0.54          | 2.01           |
| <i>Toxostoma curvirostre</i> ..... | 34          | 160.1±0.45 | 2.60±0.32          | 1.62           |
| Tarsometatarsus                    |             |            |                    |                |
| <i>Toxostoma rufum</i> .....       | 26          | 119.8±0.50 | 2.55±0.35          | 2.13           |
| <i>Toxostoma bendirei</i> .....    | 19          | 127.1±0.64 | 2.77±0.45          | 2.18           |
| <i>Toxostoma curvirostre</i> ..... | 36          | 115.0±0.37 | 2.23±0.26          | 1.94           |
| Middle toe                         |             |            |                    |                |
| <i>Toxostoma rufum</i> .....       | 22          | 99.3±0.46  | 2.16±0.33          | 2.16           |
| <i>Toxostoma bendirei</i> .....    | 21          | 104.5±0.50 | 2.30±0.35          | 2.20           |
| <i>Toxostoma curvirostre</i> ..... | 36          | 102.7±0.49 | 2.92±0.34          | 2.84           |



TABLE 10

VARIABILITY IN LIMB SEGMENT : THORACIC LENGTH RATIOS IN THREE SPECIES OF TOXOSTOMA  
(Figures represent percentage of thoracic length)

| Species                            | Humerus |            |                    |                |
|------------------------------------|---------|------------|--------------------|----------------|
|                                    | No.     | Mean       | Standard deviation | Coeff. of var. |
| <i>Toxostoma rufum</i> .....       | 25      | 130.4±0.66 | 3.29±0.46          | 2.52           |
| <i>Toxostoma bendirei</i> .....    | 21      | 134.9±0.60 | 2.75±0.42          | 2.04           |
| <i>Toxostoma curvirostre</i> ..... | 35      | 129.1±0.60 | 3.54±0.42          | 2.74           |
|                                    |         | Femur      |                    |                |
| <i>Toxostoma rufum</i> .....       | 25      | 126.1±0.62 | 3.12±0.44          | 2.47           |
| <i>Toxostoma bendirei</i> .....    | 19      | 132.2±0.77 | 3.33±0.50          | 2.52           |
| <i>Toxostoma curvirostre</i> ..... | 33      | 130.9±0.59 | 3.39±0.42          | 2.39           |

TABLE 11

VARIABILITY IN THE INTERMEMBRAL RATIOS IN THREE SPECIES OF TOXOSTOMA

| Species                            | Humerus<br>(expressed in percentage of femur) |                                                            |                    |                |
|------------------------------------|-----------------------------------------------|------------------------------------------------------------|--------------------|----------------|
|                                    | No.                                           | Mean                                                       | Standard deviation | Coeff. of var. |
| <i>Toxostoma rufum</i> .....       | 26                                            | 96.3±0.23                                                  | 1.18±0.16          | 1.23           |
| <i>Toxostoma bendirei</i> .....    | 21                                            | 101.7±0.21                                                 | 0.96±0.15          | 0.94           |
| <i>Toxostoma curvirostre</i> ..... | 36                                            | 98.8±0.19                                                  | 1.16±0.14          | 1.17           |
|                                    |                                               | Ulna<br>(expressed in percentage of tibiotarsus)           |                    |                |
| <i>Toxostoma rufum</i> .....       | 22                                            | 62.7±0.20                                                  | 0.95±0.14          | 1.52           |
| <i>Toxostoma bendirei</i> .....    | 20                                            | 66.0±0.36                                                  | 1.62±0.26          | 2.45           |
| <i>Toxostoma curvirostre</i> ..... | 35                                            | 66.8±0.17                                                  | 1.03±0.12          | 1.55           |
|                                    |                                               | Metacarpus<br>(expressed in percentage of tarsometatarsus) |                    |                |
| <i>Toxostoma rufum</i> .....       | 28                                            | 46.6±0.21                                                  | 1.10±0.15          | 2.36           |
| <i>Toxostoma bendirei</i> .....    | 20                                            | 48.2±0.23                                                  | 1.04±0.16          | 2.16           |
| <i>Toxostoma curvirostre</i> ..... | 38                                            | 49.7±0.19                                                  | 1.16±0.13          | 2.33           |
|                                    |                                               | Hand phalanges<br>(expressed in percentage of middle toe)  |                    |                |
| <i>Toxostoma rufum</i> .....       | 18                                            | 42.1±0.21                                                  | 0.87±0.15          | 2.07           |
| <i>Toxostoma bendirei</i> .....    | 23                                            | 44.8±0.23                                                  | 1.12±0.16          | 2.50           |
| <i>Toxostoma curvirostre</i> ..... | 33                                            | 41.8±0.24                                                  | 1.39±0.17          | 3.30           |

siderable; between the species intermediate in the series the differences, although slight, are—at least some of them—statistically significant.

The progressive change in the ratios indicates, within the wing, a relative increase in length of the proximal segment, the humerus, and a relative decrease in length of the distal segments. When one examines the wing segment : trunk length ratios for the same series of species (fig. 13), it is apparent that there is a shortening of the wing as a whole, in relation to body size, brought about by decrease in the length of each segment of the wing, including the proximal one. The apparent increase in length of the proximal segment

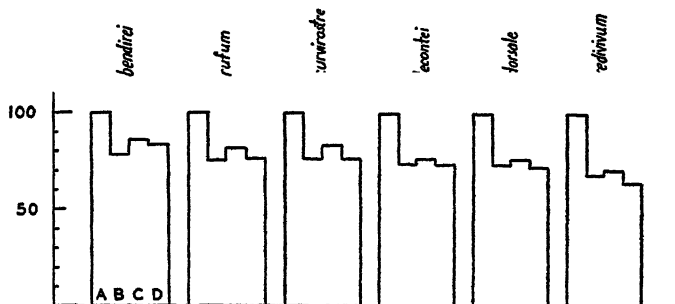


Fig. 13. Histograms illustrating wing segment : trunk length ratios in *Toxostoma*. Length of each segment is shown as percentage of length of trunk. A, trunk length; B, humerus; C, ulna; D, manus. Species arranged as in figure 12. Note that the decrease in length involves the humerus as well as the other segments.

shown by the intramembral ratios is therefore due to differential rate of decrease; the reduction in length occurs in all segments, but is more marked distally than proximally.

The same trend of progressive shortening of each element is apparent in the hand, as shown by the hand segment : thoracic length ratios (fig. 14). The differences are slight, and are strongly marked only between the extremes; but differences of a greater magnitude are hardly to be expected between members of the same genus.

#### CORRELATION OF HABITS AND WING-SEGMENT PROPORTIONS

The result of an attempt to correlate the data obtained from the various ratios, disregarding differences that are known or suspected to be nonsignificant, is a division of the series of species into three groups: (a) *bendirei*, (b) *rufum*, *curvirostre*, and (c) *lecontei*, *dorsale*, and *redivivum*.

On the evidence presented in the section on habits of thrashers, it is immediately striking that the third group, that one which shows greatest modification in the wing-segment proportions, contains just those species which seldom fly and are not strong fliers but are pronounced ground birds, making predominant use of their legs in locomotion rather than their wings. In the first group, with least modification of the wing segments, is *bendirei*, alone among the six species studied; it may be recalled that this species is most like the mockingbird, and probably most generalized in its type of flight.

The situation, then, with regard to differences in the proportions of the wing segments in these species, is what might reasonably have been expected from a knowledge of their habits (or vice versa!). The distal skeletal segments of the wing bear the flight feathers, and reduced flight ability would be expected to be accompanied by reduction in the length of these bony elements of the wing, as well as by that reduction in length of the outer flight feathers which has long been familiar to taxonomists.

The apparently lesser reduction in the hand segments of *lecontei*, shown by the intramembral ratios (fig. 12), as compared with *dorsale* and *redivivum*, stands in correlation with the slight apparent differences in the frequency

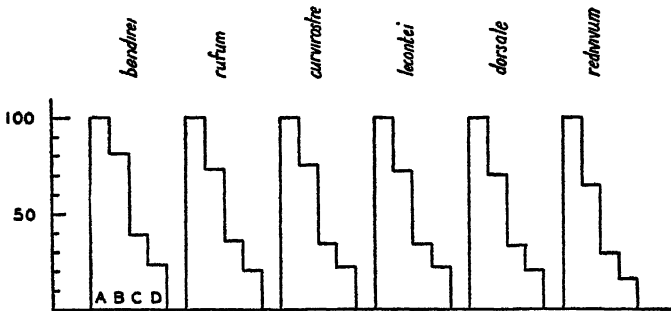


Fig. 14. Histograms illustrating hand segment: thoracic length ratios in *Toxostoma*. Length of each segment is shown as percentage of thoracic length (about  $\frac{2}{3}$  trunk length). A, thoracic length; B, metacarpus; C, phalanx 1, digit II; D, phalanx 2, digit II. Note progressive decrease in all segments, thus accomplishing the general decrease in hand length shown in figures 12 and 13.

of flight, in these species, noted in the discussion of habits (p. 349). It may also be pointed out that the length of the hand in relation to body size is least in *redivivum*, and that where possibly significant differences between *lecontei* and *dorsale* are shown, these indicate that *lecontei* is more like *rufum* and *curvirostre*, while *dorsale* approaches *redivivum* in this respect.

With regard to other mimids (fig. 15), it is to be noted that the wing skeleton in *Mimus* and *Oreoscoptes* is considerably longer than in any of the species of *Toxostoma*; of the latter, *bendirei*, most like *Mimus* in its mode of flight, approaches *Mimus* most closely in its wing-segment proportions, but differs from it principally in the possession of a very much shorter ulna and hand. In *Dumetella*, however, the wing is shorter than in *Mimus* and approaches in its proportions that of *Toxostoma rufum* and *T. curvirostre*.

Detailed comparative studies of the habits of members of these genera have not been made. However, enough is known of their locomotion to indicate that the proportions they exhibit are the ones to be expected on the principle that reduced flight ability is accompanied by a general decrease, most marked distally, of all segments of the wing.

*Dumetella carolinensis* is especially interesting in this regard. This is a bird of the thickets: its flight is mostly confined to flitting about in the brush; it rarely makes an extended flight. In correlation, it shows, when compared

with *Mimus*, the same general tendency in wing reduction as do species of *Toxostoma*.

#### PROPORTIONS OF LEG SEGMENTS IN TOXOSTOMA

Inspection of intramembral ratios of the leg segments does not immediately reveal any such clear-cut correlations as may be seen in those of the wing segments (fig. 16). It may be seen, however, that there do exist, between the several species, marked differences in the proportions. The three species for which the material was adequate for statistical treatment, *bendirei*, *rufum*, and *cur-*

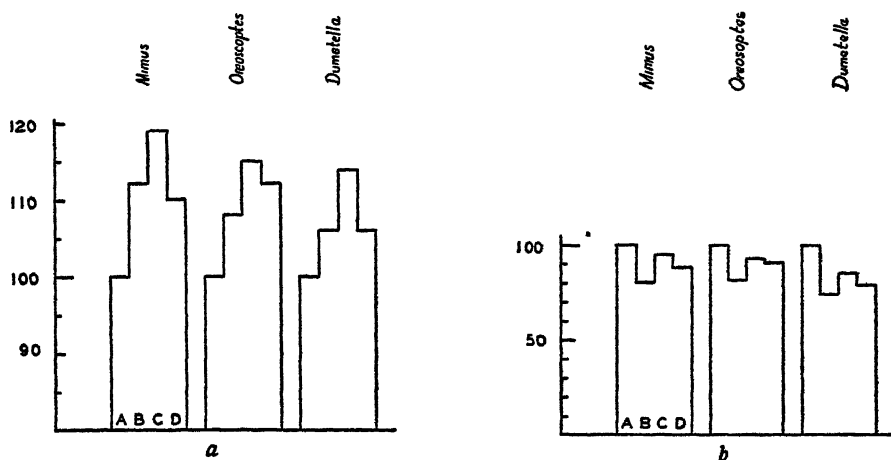


Fig. 15. a. Histograms illustrating intramembral ratios of the wing in some other mimids. A, humerus; B, radius; C, ulna; D, manus. Compare with figure 12. Note that all species of *Toxostoma* show greater relative decrease in distal segments than any of these three mimids, but that *T. bendirei* most closely approaches this pattern.

b. Histograms illustrating wing segment: trunk length ratios in some other mimids. A, trunk length; B, humerus; C, ulna; D, manus. Compare with figure 13. Note that the wing of *Dumetella* is shorter, in relation to trunk length, than that of *T. bendirei*, and similar to that of *T. rufum* and *T. curvirostre*. The wing of *Mimus* is only slightly longer than that of *bendirei*.

*virostre*, make possible nine comparisons of the three intramembral ratios, and these reveal eight significant differences (table 9). The tibiotarsus is longest in relation to the femur in *bendirei*, shortest in *curvirostre*, with *rufum* intermediate between these two. The same is true of the tarsometatarsus. The middle toe is longer in *bendirei* and *curvirostre*, shorter in *rufum*.

With fairly reliable knowledge of the variability of each ratio in three of the species, one is able to infer the probable significant differences in the other three species. In *redivivum*, the tibiotarsus is shorter, in relation to the femur, than it is in *rufum*, but longer, in the same relation, than it is in *curvirostre*. It has about the same relative length in *lecontei* and in *dorsale*, but the data are insufficient to show if in either species it is longer than in *curvirostre*.

The tarsometatarsus is of intermediate relative length in *redivivum* and in *dorsale*, as in *rufum*; it is shorter in *lecontei*, as in *curvirostre*.

The middle toe is shortest in *lecontei*, and of intermediate relative length

in *dorsale* (like *rufum*). In *redivivum* it may be either as in *dorsale* or as in *lecontei*, but it is definitely shorter than in either *bendirei* or *curvirostre*.

The same type of analysis may be applied to the leg segment: trunk length ratios, which are used to indicate the direction of changes by which the intramembral proportions are brought about (fig. 17). The femur is apparently relatively shorter in *bendirei*, *rufum*, and *curvirostre*, longer in *lecontei*, *dorsale*, and *redivivum*; but these slight differences are probably not statistically significant.

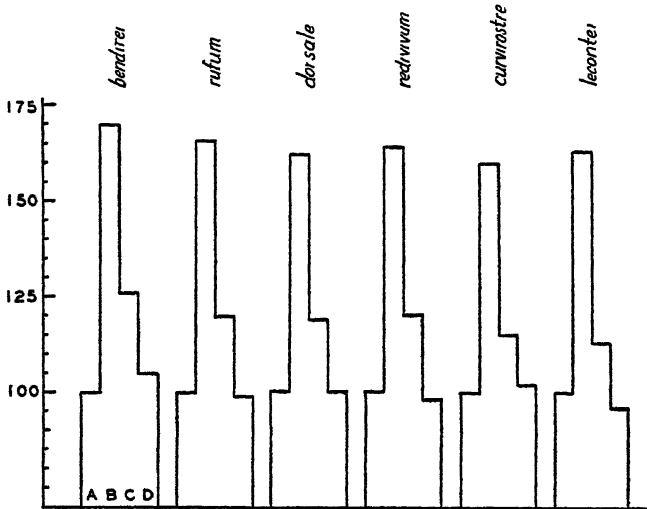


Fig. 16. Histograms illustrating intramembral ratios of the leg in *Toxostoma*. The length of each segment is shown as percentage of length of femur. A, femur; B, tibiotarsus; C, tarsometatarsus; D, middle toe. The species are arranged, from left to right, on the basis of progressive general deviation from the pattern of *Mimus* (see figure 19). (For data on variability in these ratios, see table 9.)

The tibiotarsus, longest in *bendirei*, is shortest in *curvirostre*. The low value of the ratio of tibiotarsus to femur in *curvirostre*, then, is due solely to this shortening of the tibiotarsus, since the femur is of the same relative length as in *bendirei*. In *lecontei*, *dorsale*, and *redivivum* the tibiotarsus is also short, though not as short as in *curvirostre*.

Much the same is true of the tarsometatarsus, except that in *lecontei* this segment is definitely shorter than in any other species except *curvirostre*.

The middle toe is longest in relation to body size in *bendirei*, shortest in *lecontei*, with the others intermediate, probably in the order *curvirostre*-*dorsale* and *rufum*-*redivivum*.

It is evident that, in each species, the various segments make up differing proportions of the whole leg, but in such a way that the total leg length is longest in relation to body size in *bendirei*, shortest in *curvirostre*, with the others intermediate; the leg in *rufum*, *dorsale*, and *redivivum* approaches that of *bendirei* in length; the leg of *lecontei* is almost as short as that of *curvirostre*.

## CORRELATION OF HABITS AND LEG-SEGMENT PROPORTIONS

In carrying through an analysis of the leg-segment proportions as just outlined, the relative obscurity of the results, as opposed to the situation with respect to the wing, requires some explanation. When comparison is made with *Mimus*, taken as a generalized mimid, it is evident that, within the genus *Toxostoma* in general, three sorts of change are taking place: there is a tendency to a lengthening of the femur, to a shortening of the tibiotarsus and the tarsometatarsus, and, apparently, to either a lengthening or a shortening of the middle toe. One may recall that in the wing there was to be seen only a general reduction in all elements, most marked distally.

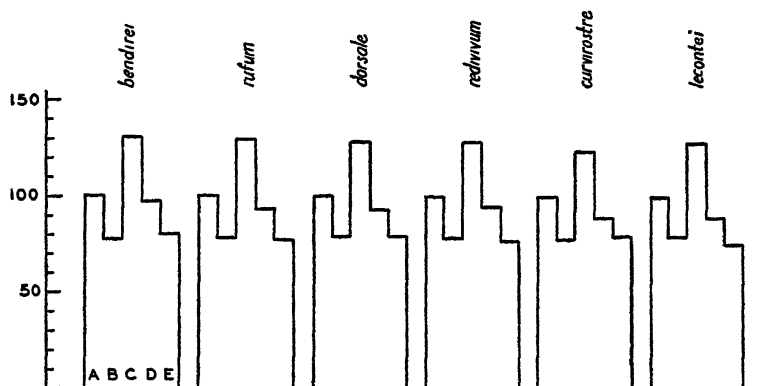


Fig. 17. Histograms illustrating leg segment : trunk length ratios in *Toxostoma*. The length of each segment is shown as percentage of trunk length. A, trunk length; B, femur; C, tibiotarsus; D, tarsometatarsus; E, middle toe. Note close similarity in all patterns, but slight differences in detail; thus, longest tarsometatarsus in *bendrei*, short tibiotarsus and tarsometatarsus in *curvirostre*, and short tarsometatarsus in *lecontei*.

The more complicated data on leg-segment proportions are therefore less readily correlated with functional differences among the species. One might reasonably expect, since the members of the genus, considered as a group, tend more to activity on the ground than do such members of the family as *Mimus*, and since the more specialized forms of the genus spend most of their time on the ground and are swift, skillful runners, that the general tendencies of change in the leg-segment proportions would be correlated with these habits.

Two facts seem to stand in contradiction to this idea. First, it is a well-known axiom of the mechanics of animal locomotion that in adaptation to the running habit there occurs a shortening of the proximal segment, and a lengthening of the distal segments, especially of the metatarsus; but this is precisely the opposite of the tendency observed in the thrashers. Secondly, cursorial forms are notably long limbed; but, as opposed to such a generalized mimid as *Mimus polyglottos*, the result of the changes in proportion within the leg is a *shorter* total leg length in relation to body size in all species of *Toxostoma*, and this is most marked among the more specialized forms of the genus.

There is another mimid, the sage thrasher (*Oreoscoptes montanus*), which is also given to ground dwelling and is as skillful and rapid a runner as are most thrashers of the genus *Toxostoma*. In this bird there is a lengthening of the whole leg in relation to body size; it has the longest leg of any of the mimids studied (fig. 18, b). The increase involves the femur, tibiotarsus, and tarsometatarsus—the situation one expects to find in running birds but does not find in *Toxostoma*. This difference between *Toxostoma* and *Oreoscoptes*

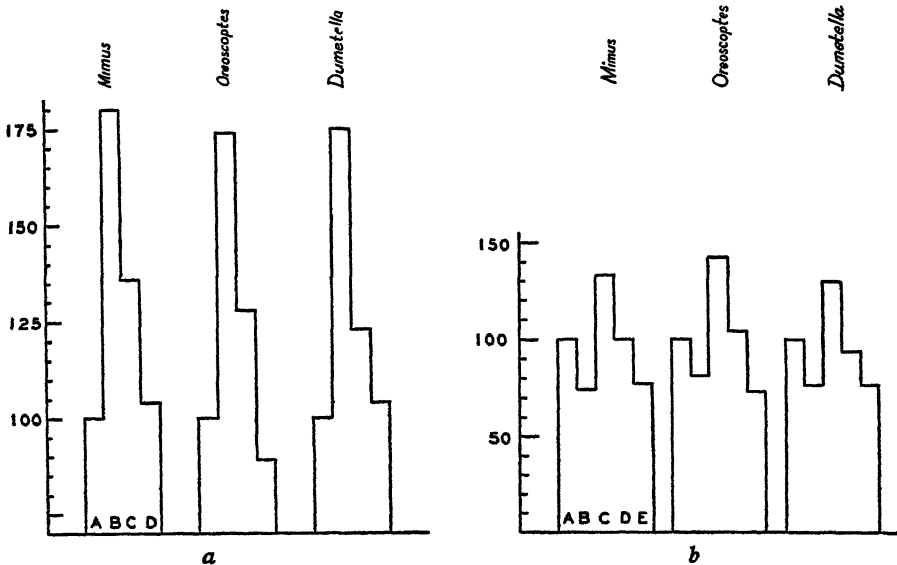


Fig. 18, a. Histograms illustrating intramembral ratios of the leg in some other mimids. A, femur; B, tibiotarsus; C, tarsometatarsus; D, middle toe. Compare with figure 16. Note that of the species of *Toxostoma*, *bendirei* most closely approaches this pattern. Note that in *Oreoscoptes* and *Dumetella*, as in all species of *Toxostoma*, the tibiotarsus and tarsometatarsus are shorter, relative to femur, than in *Mimus*.

b. Histograms illustrating leg segment : trunk length ratios in some other mimids. A, trunk length; B, femur; C, tibiotarsus; D, tarsometatarsus; E, middle toe. Compare with figure 17. Note that *Dumetella* is similar to the less modified species of *Toxostoma*, such as *bendirei* and *rufum*, when compared to *Mimus*. Note that in *Oreoscoptes*, although the intramembral proportions are as in *Toxostoma* generally, the femur, tibiotarsus, and tarsometatarsus are each considerably longer even than in *Mimus*.

may be merely evidence that the two genera have pursued quite distinctly separate phylogenetic paths. Examination of the intramembral ratios (fig. 18, a) shows that the increase in length of leg in *Oreoscoptes* is such that the proximal segment, the femur, increases in length relative to the distal segments, and these, therefore, are relatively shorter than in *Mimus*. This parallels the situation found in *Toxostoma*. In this connection it is to be admitted that the distal segments are longer in relation to the femur in *Oreoscoptes* than in any species of *Toxostoma*, being intermediate in length between those of *Toxostoma bendirei* and *Mimus polyglottos*.

One might be tempted, as I have been, to suppose that in the arboreal life typical of almost all passerine birds the proportions of the leg, cursorial in their general pattern to begin with (elongated tarsus), have been so changed

in adaptation to their different modes of life that when descendants of such forms take up ground dwelling and the cursorial habit, the direction of change necessary to produce the most efficient cursorial mechanism is reversed; that is, there must occur a lengthening, rather than a shortening, of the proximal segment, and a shortening, rather than a lengthening, of distal segments.

It is instructive here to consider leg-segment proportions in the road-runner, the extreme cursorial adaptations of which cannot, I think, be questioned. The intramembral proportions are of the same general order of magnitude as shown by *all* the mimids studied in this investigation. Actually, the tibiotarsus

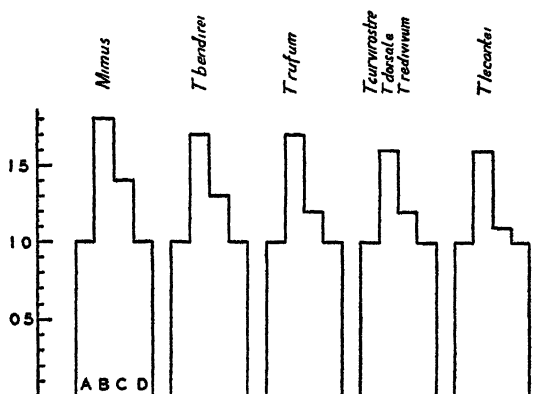


Fig. 19. Histograms illustrating intramembral proportions in the leg of *Mimus* and *Toxostoma*, based on simplified ratios calculated to the nearest 10 per cent ( $\approx 0.1$ ). Letters indicate segments as in figure 18, *a*. Note progressive decrease in relative length of tibiotarsus and tarsometatarsus in the series as here arranged. Compare with figures 16 and 18, *a*.

and tarsometatarsus are *shorter* relative to the femur than in any species of *Toxostoma* (tibiotarsus, 152 per cent of the femoral length; tarsometatarsus, 112 per cent). But in contrast to the less specialized mimids, in which these elements tend to be longer, the noncursorial relatives of the road-runner have these elements extremely short (*Coccyzus americanus*: tibiotarsus, 138 per cent of the femoral length; tarsometatarsus, 90 per cent). This has been discussed in detail elsewhere (Engels, 1938b).

A second marked tendency in habit among the species of *Toxostoma*, other than the running habit, which was pointed out in the first section of this report (p. 350) and which may be considered here, is the tendency to ground foraging and, particularly, to digging. Since the relative decrease in tarsometatarsus and tibiotarsus, and the increase in length of femur, are greater in the curve-billed (more proficient diggers) than in the straight-billed thrashers, one may legitimately attempt a correlation of the structural conditions with this habit.

The importance of the legs in digging is immediately evident in watching a California thrasher foraging. The widespread feet and the easy spring of the body on the bent legs, strongly suggest that this habit may have some



influence on the structure of the leg. Since the proportions within the leg are similar, among *Toxostoma*, to those obtaining in another running mimid, *Oreoscoptes*, it may be thought that these proportions are correlated with the running habit, and that the shorter leg of *Toxostoma* may be an adaptation to the digging habit, permitting a more favorable balance and leverage for the body while the sharp, swinging blows are being delivered with head and bill.

Among the species of *Toxostoma*, *lecontei* is farthest removed from the generalized *bendirei* type with respect to intramembral proportions of the leg (fig. 19) and is, possibly, the most rapid, skillful runner. But in respect to proportions within the leg, *bendirei* is more like *Oreoscoptes* than is any other

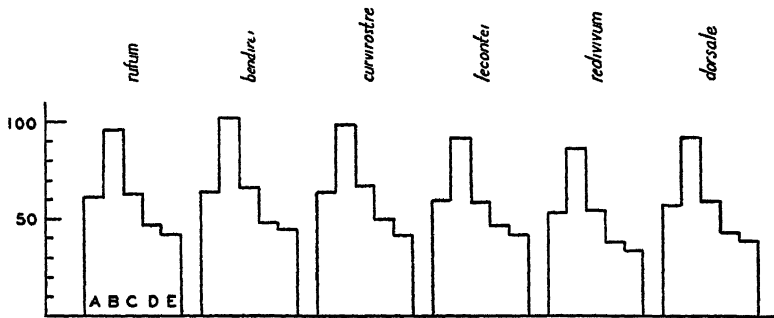


Fig. 20. Histograms illustrating the proportions of wing segments to corresponding leg segments, based on intermembral ratios, in *Toxostoma*. A, total wing in percentage of length of leg; B, humerus, in percentage of length of femur; C, ulna, in percentage of length of tibiotarsus; D, metacarpus, in percentage of length of tarsometatarsus; E, hand phalanges, in percentage of length of middle toe. The species are arranged in the taxonomic order proposed in this paper (p. 386). (For data on variability in these ratios, see table 11.)

species of *Toxostoma*. Furthermore, such an interpretation would demand that the greatest modification of the leg in relation to body size should be shown by the most proficient digger. It is *curvirostre*, however, which displays this greatest divergence; and, as has been pointed out, the digging habit is less pronounced in *curvirostre* than in *lecontei*, *dorsale*, or *redivivum*.

One correlation seems clear. It was pointed out that *Toxostoma curvirostre*, with a posture decidedly different from that of other thrashers, was less graceful as a runner. This species has also been shown to possess, in relation to body size, the shortest tibiotarsus, the shortest tarsometatarsus, and the shortest leg of all thrashers. I am certain that these two general facts, one of behavior and one of form, stand in relationship to one another. It is probable, however, that it is the short total leg length that is significant in this respect, rather than the low proportion of tibiotarsal and tarsometatarsal length within the leg, since *lecontei*, a graceful runner, closely approaches *curvirostre* in the pattern of its intramembral proportions, the tarsometatarsus being indeed even shorter than in that species. It is a correlation only that is here indicated: *curvirostre* runs with a peculiar gait because of its short legs; the adaptational significance of the short legs, if any, remains obscure.

One may be unwilling to concede that the proportions of segments within

the leg, and their length relative to body size, are without adaptational value; but it is not possible to say with any assurance, in this instance, what that value may be.

It ought finally to be emphasized that the differences here shown to exist among the mimids are comparatively slight ones and that, as shown by reference to the road-runner, they are probably not of a degree of magnitude that would affect the efficiency of the leg as a cursorial mechanism.

#### INTERMEMBRAL PROPORTIONS IN TOXOSTOMA

Consideration of the intramembral and limb:trunk ratios for wing and leg reveals that a series of species based on progressive change in the wing is differently constituted from a series based on progressive change in the leg;

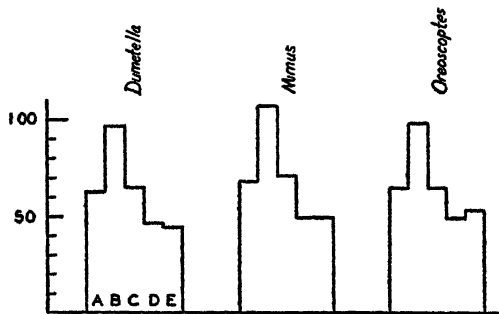


Fig. 21. Histograms illustrating intermembral ratios in some other mimids than *Toxostoma*. Symbols as in figure 20.

the two series have in common only that each begins with *bendirei*. It is clear, therefore, that differentiation in the one limb is independent, at least in some measure, of differentiation in the other. As a result, it cannot be expected that the intermembral ratios will do more than indicate a general pattern of relative length of wing to leg, characteristic of the species. This relationship is between wing and leg only, of course, and has no bearing on general body size.

The data show (figs. 20 and 21) decreasing wing length in relation to leg length in the order, *bendirei*, *curvirostre*, *rufum*, *lecontei-dorsale*, and *redivivum*. That the progressive lowering of the ratios in this series is due primarily to a shortening of the wing and not to a lengthening of the leg, is apparent from the foregoing discussions of the proportions in the wing and leg. These data, then, supplement the description previously given of wing reduction in this series of species.

#### INTERSPECIFIC RELATIONSHIPS IN TOXOSTOMA

Study of interrelationships of species in the genus *Toxostoma* was not a primary aim of the investigations reported upon in this paper; nor was the material adequate, in nature or in extent, to permit of the detailed examination that would be desirable. However, while I was studying structural adaptations

in thrashers, some information bearing upon interspecific relationships was obtained, and I have been able to draw tentative conclusions therefrom, which I now present. The information comprises some of the basic facts which in any event must be taken into consideration in judging relationships within the genus.

The ten species of *Toxostoma* appear to fall into four groups, the members of each of which I believe to be more closely related to one another than to members of any other group. These groups are:

- |                                                                                         |                                                                                         |
|-----------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------|
| (a) <i>Toxostoma rufum</i><br><i>Toxostoma longirostre</i><br><i>Toxostoma guttatum</i> | (c) <i>Toxostoma ocellatum</i><br><i>Toxostoma curvirostre</i>                          |
| (b) <i>Toxostoma cinereum</i><br><i>Toxostoma bendirei</i>                              | (d) <i>Toxostoma lecontei</i><br><i>Toxostoma redivivum</i><br><i>Toxostoma dorsale</i> |

This grouping is based upon pattern of coloration of the plumage; it seems also to be a reasonable grouping in view of the geographical distribution of the several species, and it is not inconsistent with the facts of structure and habit, so far as these are known.

#### RUFUM—LONGIROSTRE—GUTTATUM GROUP

*Plumage*.—This group of species displays a remarkable uniformity in the pattern of the coloration, even in the most minute details. The pattern is, briefly, as follows. Ventral spotting (fig. 22, A, B, C): spots long and narrow, tending toward elliptical (teardrop); smaller and narrower on sides of neck, broader on breast, longer on flanks; irregular spots on legs. Under tail coverts with central, mostly concealed, darker areas (absent in *rufum*). Middle and greater wing coverts tipped with white or pale buff, the white band preceded by an indistinct band of dusky. Remiges, upper surface of outer web similar in color to general tone of back, inner web darker (black, less brown). Outer rectrices indistinctly tipped with buff or buffy white.

The three species differ from one another in general coloration; in *rufum* the ventral spots are brown or dusky, the dorsum is cinnamon rufous or tawny rufous in color. In *longirostre* and in *guttatum* the ventral spots are black; the dorsum is darker and duller in *longirostre* (more nearly brown, less rufous); in *guttatum* it is brighter, more nearly as in *rufum*.

*Color of soft parts*.—The iris is bright yellow in *rufum* and in *longirostre*; its color in *guttatum* has not been recorded. The lining of the mouth is yellow in *rufum*; its color in the other two species is unknown.

*Geographic distribution* (fig. 23, 1, 2, 3).—The breeding ranges of the species are separated completely from one another. The distribution suggests that of an *Artenkreis*.

*Structural details*.—Of only one species of this group, *rufum*, were skeletons and alcoholic specimens available. Three study skins of *longirostre* were examined, two of *guttatum*; also, use was made of the average measurements given by Ridgway (1907, pp. 188, 191, 193).

*Rufum* and *longirostre* are about equal in size; *guttatum* is considerably smaller than either. The bill is of about equal relative length in *longirostre* and in *guttatum*; in each it is slightly longer relative to general body size than in *rufum*. In *rufum* the bill is nearly straight; it is slightly curved in *longirostre* and in *guttatum*; the curvature is more pronounced in the latter.

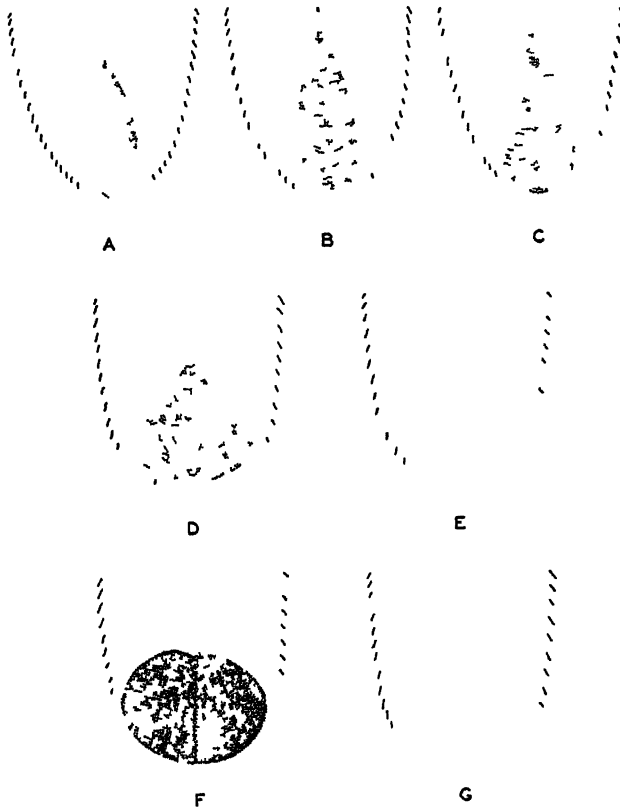


Fig. 22. Tips of breast feathers in *Toxostoma*; semidiagrammatic. Note shape of spots. A, *rufum*; B, *longirostre*; C, *guttatum*; D, *cinereum*; E, *bendirei*; F, *ocellatum*; G, *curvirostre*. The remaining species of the genus lack these spots.

The wing is slightly shorter in relation to body length in *longirostre* and in *guttatum* than in *rufum*; in *guttatum* the tail also is shorter, so that the wing: tail ratio is about as in *rufum*. The leg appears to be similar in all three, though there is a suggestion of reduction in tarsal and middle toe lengths in *guttatum*.

In view of the general tendencies of change within the genus, mentioned in previous sections of this paper, the members of this group, on the basis of degree of specialization, should be arranged in the following order: *Toxostoma rufum*, *Toxostoma longirostre*, *Toxostoma guttatum*. This arrangement is, indeed, the traditional one, as employed by Ridgway (1907, pp. 187-193) and, more recently, by Hellmayr (1934, pp. 295-296).

## CINEREUM-BENDIREI GROUP

*Plumage*.—Species of this group differ from those of the preceding group chiefly in having the ventral spots triangular rather than elliptical (fig. 22, D, E). The entire pattern is, briefly, as follows. Ventral spots: triangular or wedge shaped; smaller on sides of throat, larger and most numerous on chest; sparse on breast, sides, and flanks. Middle and greater wing coverts: tipped

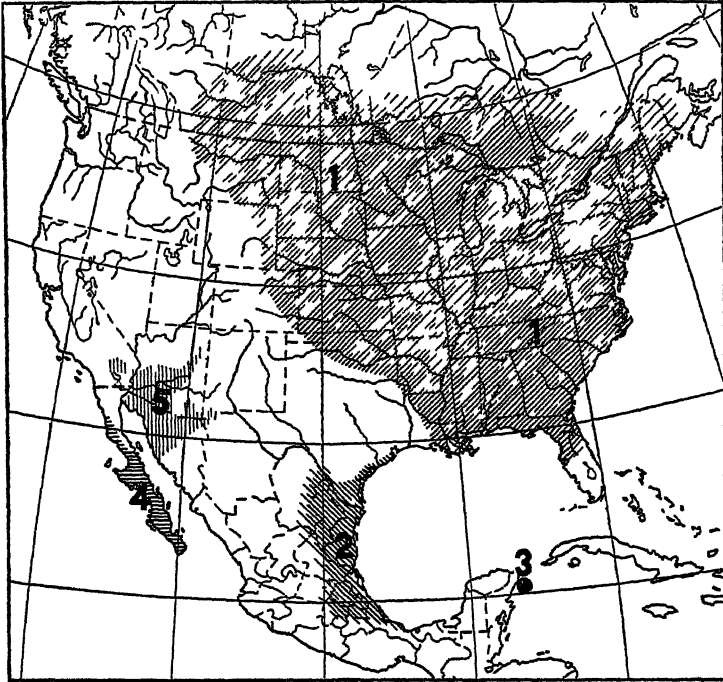


Fig. 23. Map showing distribution of the *rufum*-*longirostre*-*guttatum* group of the genus *Tachycineta* and of the *cinereum*-*bendirei* group. 1, *rufum*; 2, *longirostre*; 3, *guttatum*; 4, *cinereum*; 5, *bendirei*. The northern limits of the range of *rufum* and the western limits of the range of *longirostre* are uncertain. This map, and the two following, are not intended to show local details of distribution.

with white, the white band not bordered by dusky; indistinct in *bendirei*. Remiges with upper surfaces of outer web not lighter than inner web, but edged with whitish. Inner web of outer rectrices broadly tipped with white, outer web narrowly tipped; white area narrower in *bendirei*. In *cinereum* the ventral spots are black or blackish brown, and stand out sharply; in *bendirei* they are light grayish brown in color and are very pale and indistinct except on the upper chest, where they are narrow and sharply defined. The general color of the dorsum is grayish brown in each species, but paler in *bendirei*.

According to Ridgway (1907, p. 195), the markings on the underparts in young *cinereum* are smaller and more linear; this would suggest that the pattern in the young was nearer that of the preceding group than that of the

adult. I find, however, that although the spots may be narrower on the chest, still they are truncate throughout, and definitely wedge shaped. Transition from the *rufum* type is to be found both in juvenal and adult plumages in a few linear, nearly elliptical spots on the abdomen.

In *bendirei*, the ventral spots are decidedly longer and narrower in the juvenile, more nearly like those on the sides of the throat and the upper chest of the adult; they are long, narrowly wedge shaped, rather than short, broadly wedge shaped, and in this respect *bendirei* is nearer the *rufum* type.

*Color of soft parts.*—The iris is yellow in each species. The lining of the mouth is yellow in *bendirei*; in *cinereum* its color is unknown.

*Geographic distribution* (fig. 23; 4, 5).—The species occupy adjacent but separated areas. *Cinereum* shares part of its range with *lecontei*; in a limited area near 30° north latitude in Lower California, it probably occurs with *redivivum*. In Arizona and Sonora, *bendirei* occurs with *curvirostre*, *lecontei*, and *dorsale*. This situation is discussed in connection with the two following groups.

*Structural details.*—These two species are similar to each other in general body size; wing slightly shorter relatively in *cinereum* (about as in *rufum*); tail shorter in *cinereum*, and bill longer (both about as in *guttatum*); bill in *bendirei* about as in *rufum*, but more curved.

Both in *cinereum* and in *bendirei* the suprameatic process is very broad, with the lateral edge rolled over toward the tip (fig. 6, B, C); this is distinctly different from its construction in *rufum*, *curvirostre*, or any member of the *lecontei-redivivum-dorsale* group.

#### OCELLATUM-CURVIROSTRE GROUP

*Plumage.*—This group, like the preceding one, contains two members, one of which shows intense, the other pale coloration. The two groups differ markedly in the shape of the ventral spots (fig. 22, F, G). The pattern is as follows. Ventral spots subrounded or orbicular; larger on chest and breast, smaller on upper abdomen; longer and more irregular on flanks. Under tail coverts broadly tipped with white, this preceded by a prominent black bar in *ocellatum*; white tip indistinct and black bar absent in *curvirostre*. Middle and greater wing coverts tipped with triangular spot of white, the apex of which is directed proximally along the shaft; less distinct and more irregular in *curvirostre*, but tending toward this pattern. Remiges edged with buffy or whitish (as in the *cinereum-bendirei* group). Rectrices tipped with white, this area broader on the inner than on the outer web (as in the *cinereum-bendirei* group); the white area narrow in *ocellatum*.

In *ocellatum* the ventral spots are black and very prominent; the dorsum is deep brown in color, tending to olive. In *curvirostre* the spots are pale brownish gray, sometimes slaty, and inconspicuous, especially in worn plumage; the dorsum is grayish brown.

The plumage of young *ocellatum* is not known. In *curvirostre* the spots on the underparts of the young are not subrounded as in the adult, but are longer

and more streaklike. Some are broadly rounded toward the distal end of the feather and are essentially of the *rufum* type; others are wedge shaped, of the *cinereum* type. Juvenal *bendirei* and *curvirostre* are so similar in appearance that they may be distinguished from one another with certainty only by the black tongue of the latter.

*Color of soft parts.*—The iris is between yellow and orange in *curvirostre*; in *ocellatum* the color is not known. The mouth is yellow in *curvirostre*, as in *rufum* and *bendirei*, but is distinguished from these by having the tip of the

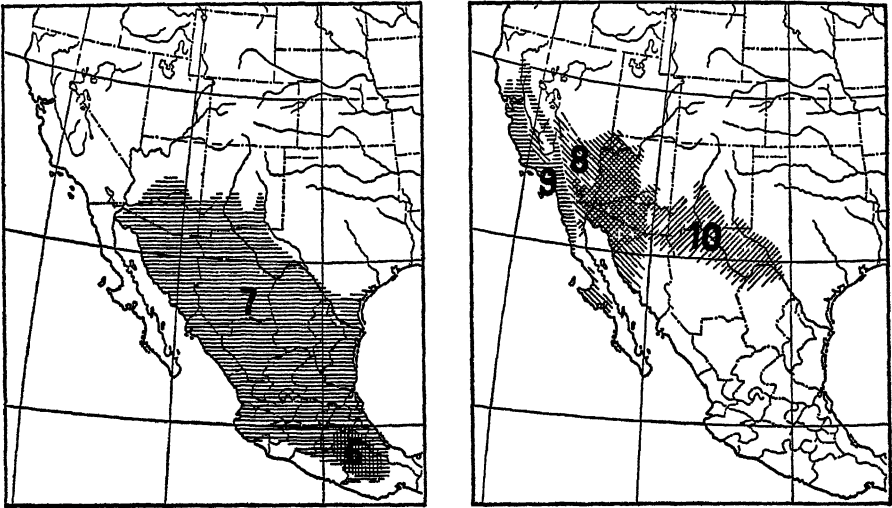


Fig. 24. Maps showing distribution of the *ocellatum*-*curvirostre* and the *lecontei*-*redivivum*-*dorsale* groups of the genus *Toxostoma*: 6, *ocellatum*; 7, *curvirostre*; 8, *lecontei*; 9, *redivivum*; 10, *dorsale*. *Curvirostre* is undoubtedly absent over much of the territory shown; but there are records for each of the states of Mexico shaded on this map. It is intended only to show the relation between the ranges of *curvirostre* and *ocellatum*.

tongue blackish; this black tongue characterizes the nestling as well as the adult. The color of the mouth in *ocellatum* is not known.

*Geographic distribution* (map, fig. 24).—The range of *ocellatum* is enclosed within the range of *curvirostre*. The range of the former is greatly limited, however, being restricted to the southernmost portion of the very extensive range of the latter. It would appear as if the range of *curvirostre*, subsequent to the differentiation of the two species, had been extended to include that of *ocellatum*. If these two species actually are closely related, as I think they are, it is to be expected that they are ecologically segregated in the area of their common range in north-central Mexico, as members of the succeeding group are in the Southwest (see below). Unfortunately, nothing is known of the habits and habitat preferences of *ocellatum*.

*Ecologic distribution.*—Comparison of the maps showing geographical distribution of the species of *Toxostoma* (figs. 23 and 24) indicates that *curvirostre* overlaps the geographical range of members of each of the other three groups of related species. Thus, it occurs with *longirostre* in northeastern

Mexico and the lower Rio Grande Valley in Texas; in Arizona and Sonora it is found together with *bendirei*, and here also with *lecontei* and *dorsale*; finally it inhabits, with *dorsale*, southern New Mexico, the trans-Pecos region of Texas, and adjacent parts of Mexico.

I have studied this situation in the field only in Arizona and have no information from other regions; but it is likely that the conditions seen in Arizona also exist elsewhere. Of the four species occurring on the Lower Sonoran deserts in southern Arizona, *curvirostre* is easily the most tolerant and wide-ranging with respect to habitat. *Dorsale* and *lecontei* are greatly restricted, the former to the mesquite thickets, the latter to open areas with scattered bush and with loose, sandy soil. *Bendirei* seems to prefer the margins of the thickets, but ranges out from this typical habitat more commonly than do the former two species from theirs. *Curvirostre* covers all such areas in its range. It completely overlaps *bendirei*, so that wherever the latter occurs, *curvirostre* is certain to be found. It is most rare in the denser thickets, where *dorsale* abounds, but is commonly met with in the marginal, less densely covered areas, out into which *dorsale* ranges freely. One habitat, however, remains almost solely for *curvirostre*—the cactus-covered mesas, hills, and canyons—and here *curvirostre* occurs in greatest abundance. There is thus at least an indication of ecological segregation; *curvirostre* is most numerous in a habitat which covers extensive areas of Lower Sonoran desert and in which *dorsale* is never met with, and *lecontei* and *bendirei* but infrequently.

*Structural details.*—Comparison of the members of this group is restricted to such facts as are shown by examination of skins. In general body size, *ocellatum* and *curvirostre* are about equal; *ocellatum* appears larger by virtue of its distinctly longer tail. The wing is of about the same relative length in each. The bill is slightly longer in *ocellatum*. Both in *curvirostre* and in *ocellatum* the curvature of the bill is greater than in any member of the preceding groups. The tarsus is relatively longer in *ocellatum*, about as in the five species already discussed.

From the foregoing description, it is seen that the *ocellatum*-*curvirostre* group differs from each of the preceding groups in two respects: the large size and rounded shape of the ventral spots, and the greater curvature of the bill. Each of these is to be looked upon as a departure from a generalized type; the group therefore should follow the *rufum*-*longirostre*-*guttatum* and the *cinereum*-*bendirei* groups in systematic treatment. *Curvirostre* is more extreme than *ocellatum*, chiefly in the fading of its coloration, but also in its shorter tarsus. Except for the difference in color, the differences between these two species are no greater than those obtaining between the species *rufum* and *guttatum*.

In the lists of Ridgway (1907, pp. 195–199), and Hellmayr (1934, pp. 290–297), *ocellatum* follows *guttatum* and precedes *cinereum*; *curvirostre* follows *bendirei*. This arrangement fails to take cognizance of such similarities between *ocellatum* and *curvirostre* as I have pointed out; nor can I perceive any logical basis for it.



## LECONTEI-REDIVIVUM-DORSALE GROUP

*Plumage*.—The members of this group are marked off sharply from other species of *Toxostoma* by the complete absence of spots or streaks on the underparts. This gives a uniformity to the pattern of coloration which accounts for most of the general similarities obtaining among the three species. The pattern, briefly, is as follows. No ventral spotting whatever, not even in juvenal plumage. Middle and greater wing coverts indistinctly tipped. Rectrices broadly tipped with pale gray-brown in *lecontei*, with buffy brown in *dorsale* and *redivivum*; narrow and indistinct in the latter.

The general coloration is as follows. In *lecontei*, chin and throat whitish; upper breast and sides very pale grayish brown; lower breast and abdomen dull whitish, passing from light buff to deep buff or tawny in region of crissum and under tail coverts. In *redivivum*, pattern similar, but upper breast and sides darker, more brown; lower breast and abdomen buff to cinnamon buff (similar in color to crissum in *lecontei*) and becoming cinnamon in region of crissum and under tail coverts. In *dorsale*, more uniform; all grayish brown except for whitish throat and deep rufous crissum and under tail coverts. Dorsal surface more or less uniform in all three species and darker than the ventral surface. Dorsum grayish brown in *lecontei* and *dorsale*, but darker in the latter, and deep gray-brown in *redivivum*.

*Color of soft parts*.—Iris brown (*redivivum*, *dorsale*) or reddish brown (*lecontei*). Lining of mouth whitish or flesh color. Young of all three species have the yellow mouth characteristic of other species. The iris, similarly, is at first gray, then ivory; the pigment first appears as an indistinct straw-yellow band around the pupil, as in other species. The brown or reddish brown color of the adults is acquired sometime after the postjuvenile molt.

*Geographic distribution* (fig. 24).—The range of *redivivum* is separated from the ranges of *lecontei* and of *dorsale*; the ranges of the latter two overlap, in part. The ranges of *redivivum* and *lecontei* are contiguous along a more extensive border than those of *redivivum* and *dorsale* and overlap slightly; but either *lecontei* or *dorsale* may be said to replace *redivivum* geographically.

*Ecologic distribution*.—*Redivivum* is rather strictly limited to the Upper Sonoran life zone; *lecontei* and *dorsale* occur only in the Lower Sonoran life zone. More specifically, each species is closely confined within its life zone to a particular type of habitat. *Redivivum* occupies the chaparral, *dorsale* the mesquite thickets, and *lecontei* the sandy-surfaced areas with scattered bush. Everyone who has studied these birds in the field has been impressed, as I was, by the distinct habitat preferences of each of these species. (See, for example, for *lecontei*: Mearns, 1886; Merriam, 1895; Gilman, 1902 and 1909; and, especially, Grinnell, 1933. For *redivivum*: Grinnell, 1917. For *dorsale*: Mearns, 1886; Gilman, 1902 and 1909; and Grinnell, 1914.)

The mesquite thickets of the Lower Sonoran life zone form a habitat closely comparable to the chaparral of the Upper Sonoran life zone. Grinnell (1917, p. 432) has drawn a picture of the habitat requirements of *redivivum* which

might be applied directly to *dorsale*: "... always dependent upon vegetational cover; and this cover must be of the chaparral type, open next to the ground, with strongly interlacing branch-work and evergreen leafy canopy close above—not forest undergrowth, or close-set, upright stems as in new-growth willow, or matted leafage as in rank-growing annual herbage." This is, essentially, a description of mesquite thickets in relation to the requirements of *dorsale*.

The habitat requirements, or preferences, of *lecontei*, however, are of quite a different sort, in which sandy-surfaced terrain, grown sparsely to small bushes, with far-flung open spaces between, is to be emphasized.

That *lecontei* is able to maintain itself successfully in mesquite thickets, however, is indicated by the observations of Grinnell (1923, p. 103) in Death Valley, where Leconte thrashers were found only in the mesquite association. Grinnell's interpretation is that, because the crissal thrasher, which is "the species of pronounced adaptation to that [mesquite] association," is absent from Death Valley, "the Leconte has been able to take over the mesquite habitat because there is no rival thrasher there." Another important factor is the probable scarcity of habitable ground for the Lecontes on the floor of Death Valley *outside* of the mesquite association. In other words, *dorsale* is cut off from Death Valley, undoubtedly through the absence of suitable habitats over the extensive high desert area surrounding the valley. But this area is no barrier to *lecontei*; in fact, most of it is probably typical *lecontei* habitat. In the bottom of the valley, however, where most of the vegetational associations are essentially sterile of bird life, typical *lecontei* habitat is wanting; but the mesquite association, because of the absence of *dorsale*, is available to *lecontei*, and has been appropriated.

This involves no contradiction of the essential dissimilarity in the preferred habitats of *lecontei* and *dorsale*. Individuals of the two species may frequently be seen together on marginal land bordering the dense thickets, when this marginal land is suitable to *lecontei* (for example, covered with *atriplex*). Again, in an area like the upper San Joaquin Valley, *lecontei* is found concentrated along the draws where *atriplex* grows most thickly and provides nesting sites and shelter for the birds. But they range freely out into the open land; and they occur, in numbers, in places where there is no concentration of bush. If predominant conditions over the greatest part of their range indicate anything, it is that Leconte thrashers prefer country sparsely grown to small bushes (discontinuous cover) rather than to dense thickets (continuous cover).

*Redivivum* and *dorsale*, to repeat, are ecological counterparts, living in analogous habitats in adjacent life zones and in adjacent geographic areas; *lecontei*, occurring in the same life zone as *dorsale* and over the same geographic area in part, occupies a distinctly different type of habitat.

*Structural details.*—*Lecontei* and *dorsale* are similar in body size to each other (slightly larger than *bendirei*, smaller than *rufum* or *curvirostre*); *redivivum* is the largest of all species of the genus. The tail is shorter, rela-

tively, in *redivivum* (about as in *cinereum*, *bendirei*, or *curvirostre*) and is longer in *dorsale*, which has, relatively, the longest tail of any thrasher, except possibly *ocellatum*. The bill is of approximately equal relative length in *lecontei* and in *redivivum*, but longer in *dorsale*; in each it is longer than in any thrasher belonging to the other groups, and has a greater curvature.

In each of these three species, the proportions of the wing segments indicate reduction in the wing; this is associated with their common aversion to flight and preference for running as a means of locomotion. It has been pointed out that *dorsale* more nearly resembles *redivivum* in these respects than does *lecontei*. *Lecontei* differs from the other two also in its shorter tarsus.

Attention already has been directed to the great reduction in width of the temporal fossa in these three species, and to the decrease in size of the external mandibular muscle. The suprameatic ridge and process are entirely similar in *dorsale* and *redivivum*, but in *lecontei* show a difference, difficult of description but obvious in the specimens (see fig. 6, p. 356).

*Interrelationships within the group.*—There is prevalent in the literature an opinion that *lecontei* and *redivivum* are more nearly related to each other than either is to *dorsale*, that, indeed, *lecontei* has but recently been differentiated from *redivivum*. I cannot agree with this opinion. Throughout the previous discussions of structure, proportions, habits, and habitat preferences, time and again the greater degree of similarity between *dorsale* and *redivivum*, and the deviation of *lecontei*, have been pointed out. Indeed, there is but one significant character apparent to me in which *lecontei* is nearer *redivivum* than is *dorsale*, and that is in the coloration of the eggshell, which is a clear, unspotted blue in *dorsale*, although it is spotted in *lecontei* and in *redivivum* (as also in all other species of *Toxostoma*!). But again, in an associated habit, that of nest building, *dorsale* is nearer *redivivum*; the nest of *lecontei* is decidedly different from those of the other two. None of these characters probably permit one to go so far as to assert a greater degree of affinity between *dorsale* and *redivivum*; but I am convinced that these two are as closely related as are *redivivum* and *lecontei*.

*Summary.*—The species of this group agree among themselves and differ from all other thrashers in the absence of ventral spotting even in the juvenal plumage; in having the iris brown, rather than yellow; the lining of the mouth whitish or flesh colored, rather than yellow; in the extreme curvature of the bill and, in association, reduction of the external mandibular adductor muscle and the temporal fossa, and the large size of that portion of the pterygoid muscle which inserts on the basitemporal; and in the reduction of the wing, as shown by proportions of the wing skeletal segments, associated with infrequent flight and the running habit. All these are extreme developments within the genus; the members of this group are the most specialized species of thrashers. Within the group, *dorsale* shows the greatest curvature of the bill, *redivivum* the greatest reduction in the wing, and *lecontei* an extreme modification of the leg-segment proportions. The three species are separated in their ranges, in part geographically, in part ecologically. *Redivivum* and

*dorsale* are ecological counterparts in adjacent life zones; *lecontei* prefers a different type of habitat. *Dorsale* is at least as closely related to *redivivum* as is *lecontei*.

### DISCUSSION AND SUMMARY

Thrashers of the genus *Toxostoma* exhibit two marked tendencies of behavior: toward ground foraging, and toward running rather than flying as a means of locomotion.

Among the less specialized members of the genus, such as *rufum* and *ben-direi*, foraging consists mostly in the searching out, on the ground, of insects, and fallen seeds and berries. Some insects are obtained from beneath the surface by pecking, poking, or hammering the bill into the ground. The more specialized forms, such as *redivivum*, *lecontei*, and *dorsale*, when they excavate holes, actually dig insects out of the earth, tunneling out, as they dig, ground spiders, crickets, and other animals of like habitat.

Structural characters associated with the digging habit involve the bill, the skeleton, chiefly of the head, and the musculature of the head and neck. The major structural adaptation is a marked curvature of the bill. The bill is relatively straight in those forms which do not dig, but is strongly decurved in digging forms. With a curved bill, essentially the same movements as those used in poking or hammering a straight bill into the ground would break up the dirt caught within the arc of the bill and thus accomplish the excavation of holes. Therefore, only slight modifications in behavior are necessary to change a ground-pecking form into a digging form, once the digging tool, the curved bill, is evolved.

Curvature of the bill is a result of increase in bill length relative to body size. This increase in length involves chiefly the distal part of the bill, which is slightly curved even in the generalized forms, for example, *rufum*.

Because the increase in length is chiefly in the distal part of the bill, the mandibular symphysis is relatively longer in the curve-billed forms. This is of mechanical advantage in digging; it is not, however, causally related to the digging habit.

In an extremely specialized form, such as *redivivum*, the mass of that portion of the pterygoideus muscle which extends from the palatine and the pterygoid to the base of the skull is nearly as large as that extending from the palatine and the pterygoid to the mandible. This is considered to be an adaptation which assures greater rigidity and strength to the upper jaw in resisting the strain put upon the bill in digging. Another specialization in the musculature consists in the lengthening of the flexor capitis inferior and longus colli anterior muscles. This arrangement gives greater power and range to the downstrokes of the head and neck in digging. There is an associated fusion of the thoracic vertebrae which provides for a more rigid base from which the action of the neck flexor can proceed.

All mimids exhibit the chief mechanical adjustment, with respect to the pterygoideus muscle, of advantage in digging—namely, the presence of muscle bundles extending from the pterygoid to the base of the skull; these are

absent in other passerines. All species of *Toxostoma* have the flexors of the head and neck longer than do other mimids, which are typically passerine in this respect. In the essential muscular mechanisms, then, all thrashers are preadapted to the digging habit. This habit develops in conjunction with the development of a curved bill, which is itself the result of an increased relative length of the bill. The adaptations of the curve-billed thrashers to the digging habit consist in the elaboration of the inherited muscular mechanism, that is, chiefly increase in the mass of the several muscles concerned, and fusion of the thoracic vertebrae, probably together with subtle psychological adjustments.

A structural peculiarity indirectly related to the digging habit, but directly related to bill curvature, involves the superficial portion of the external mandibular adductor muscle and the temporal fossa of the skull, from which the muscle arises. Ordinarily, part of this muscle is of primary importance in retraction of the lower jaw—a normal jaw movement in passerine birds. But retraction is mechanically disadvantageous in curve-billed forms, because it tends to separate upper and lower bills at their tips; in curve-billed species, in adaptation thereto, there is a marked reduction of that part of the external adductor which is chiefly accountable for retraction and, in association, a shifting upward of the suprameatic ridge and a diminution in the extent of the temporal fossa. The differences among the species of *Toxostoma* in this respect are proportional to the degree of curvature in the bill.

From the foregoing, it is apparent that the structural characters associated with the digging habit are of three sorts, as follows. (1) *Preadaptations*: peculiarities of musculature of advantage in digging, but arising before the development of the digging habit, as evidenced by their occurrence in other mimids (pterygoideus) or in nondigging thrashers (flexors of head and neck). (2) *Incidental adaptations*: lengthening of the mandibular symphysis, of advantage in digging, but causally related to increased length of bill. (3) *Primary adaptations*: a curved bill, the result of increased relative bill length; and the elaboration of preëxisting muscular mechanisms. Besides, there are *concomitant adaptations*: reduction of the external mandibular adductor muscle, in direct adaptation to the curved bill.

In association with the second major tendency in the behavior of thrashers, the preference for running and aversion to flight as a means of locomotion, there are well-marked modifications in the structure of the wing, chiefly in the proportions of the wing segments.

All members of the family Mimidae have the wing more or less rounded, that is, not pointed; in the thrashers this is especially noticeable, and, moreover, the wing is relatively short. The length of the wing skeleton is less in relation to body size in all thrashers than it is in *Mimus polyglottos* or probably than in any other mimid except *Dumetella*. It is especially short in those thrashers which seldom fly, such as *lecontei*, *redivivum*, and *dorsale*. This indicates that there is a reduction in the length of the wing associated with aversion to flight and reduction in flight ability. Various ratios show that the reduction occurs in all segments of the wing; however, it is greater in the distal

segments, so that the proximal segment becomes longer relative to the distal ones. The distal segments bear the flight feathers; it is by a reduction in length of the outermost of these that the rounded wing which is a general characteristic of the weaker fliers is brought about. It appears, therefore, that reduction of flight ability is accompanied by a general reduction in the wing, involving both the exoskeleton (the flight feathers) and the endoskeleton (the wing bones), and that this reduction is relatively greater distally than it is proximally. Here evolution reverses its steps, since in the phylogenetic development of the wing there was almost certainly a lengthening of the limb skeleton which involved chiefly the distal parts.

With respect to the leg, members of the genus *Toxostoma* have a longer femur, but a shorter tibiotarsus and tarsometatarsus, than do other mimids. There are slight differences among the species of *Toxostoma*; the author was unable to correlate them with differences in behavior. They are probably not large enough to affect the efficiency of the leg as a cursorial mechanism.

Wing: leg ratios give a characteristic pattern for each species. These are not of special functional significance, since the same sort of pattern may be the result of change in either limb.

Specializations toward the digging habit, on the one hand, and toward terrestrial locomotion, on the other, are essentially independent phenomena, although they are usually associated with one another among the several species of thrashers. In one species, *curvirostre*, however, there is little reduction in the wing, but the adaptations to digging are quite evident.

In studying structural modifications among the species of *Toxostoma*, it was noticed that *lecontei*, *redivivum*, and *dorsale* frequently showed, among themselves as a group, a degree and kind of specialization which set them apart from other species. This led to an inquiry concerning the interspecific relationships in the genus.

It is suggested that the genus *Toxostoma* is made up of four distinct groups of related species. The chief, and most practical, means of recognizing the groups is through the pattern of coloration of the plumage, mainly by the presence or absence of ventral spots, and their shape when present. These spots have a teardrop shape in the *rufum-longirostre-guttatum* group; they are wedge shaped in the *cinereum-bendirei* group, and orbicular in the *ocellatum-curvirostre* group. In the juvenal plumage of the latter two groups, the spots are more nearly like those of the first group than they are in the adult plumage. The spots are pale in one member of each of two groups (*bendirei* and *curvirostre*); in the *lecontei-redivivum-dorsale* group they are entirely absent, even in the juvenal plumage. The latter group differs from all others, also, in having the lining of the mouth flesh colored rather than yellow and in having the iris some shade of brown in color rather than yellow.

With regard to geographic distribution, there is considerable overlapping of the respective ranges of the groups; for example, four species representing three groups occur in southwestern Arizona. But within each group there is either complete geographic segregation of all members (*rufum-longirostre-*

*guttatum*; *cinereum-bendirei*), or one member is restricted to a small area at the extremity of the range of another (*ocellatum-curvirostre*), or the members are separated from one another partly geographically, partly ecologically (*lecontei-redivivum-dorsale*). Where overlapping of geographic ranges occurs as between groups, and where this condition has been studied in the field, evidence has been found to indicate at least a partial segregation, ecologically, of the species concerned. The fact of ecological segregation of species over a common geographical area leads one to infer the presence of distinctive adaptations in each species to the special requirements of its preferred habitat. Among the species of *Toxostoma* such adaptations, which probably are subtle, could not usually be determined definitely.

In structural adaptation, the members of the *lecontei-redivivum-dorsale* group differ from the members of other groups in having the bill longer and more strongly curved, with attendant extreme modification of the jaw muscles, especially of the external mandibular adductor. The reduction of the wing has proceeded farther in this group than in others; this is directly correlated with the habits of members of this group. In *lecontei* the wing reduction is somewhat less marked than in *dorsale* or *redivivum*, perhaps in correlation with its preference for a more open habitat and more frequent flight. The proportions of the leg, also, are different in *lecontei*; *dorsale* is more like *redivivum*. In the structure of the suprameatic ridge and in the thoracic portion of the vertebral column, *lecontei* again differs from *dorsale* and *redivivum*. It is therefore contended, contrary to the prevailing opinion, that *lecontei* is not more closely related to *redivivum* than is *dorsale*.

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# THE PINYON MOUSE (*PEROMYSCUS TRUEI*) IN NEVADA, WITH DESCRIPTION OF A NEW SUBSPECIES

BY

E. RAYMOND HALL AND DONALD F. HOFFMEISTER

(Contribution from the University of California Museum of Vertebrate Zoology)

IN NEVADA, we have generally found mice of the species *Peromyscus truei* on rocky areas which support a growth of pinyon trees. Pinyons without rocks and rocks without pinyons seem not to provide habitats suitable to the mice. Specimens assembled from various localities in the more elevated, northeastern part of the state agree among themselves, and differ from mice of this species from other areas to a degree which in our opinion warrants subspecific distinction for these animals. The name proposed and the differential characters are given below.

## *Peromyscus truei nevadensis*, new subspecies

*Type*.—Female, adult, skin with skull, no. 68479, Mus. Vert. Zool.;  $\frac{1}{2}$  mi. W Debbs Creek, 6000 feet, Pilot Peak, Elko County, Nevada; July 20, 1935; collected by A. E. Peterson; original no. 144.

*Range*.—Northeastern Nevada; from central Elko County south to northeastern Lincoln County, and from the Utah boundary west, north of Nye County, to eastern Pershing County (see map, fig. 1).

*Diagnosis*.—Size: large; body relatively as well as actually long. Color: pale; upper parts with a small amount of blackish and with reddish or buff color of a markedly light tone. Skull: large; rostrum relatively long; auditory bullae moderately inflated.

*Comparisons*.—From *Peromyscus truei truei*, of which we employ specimens from northern New Mexico, northern Arizona, and southern and western Nevada, *nevadensis* differs as follows: Total length greater; body longer; length of tail averages 86 as opposed to 95 per cent of length of head and body; color paler, resulting from less blackish and a lighter tone of cinnamon in upper parts; skull averages larger in every measurement taken except least interorbital constriction, palatine slits, and diastema, which are about the same as in *truei*; rostrum relatively as well as actually longer; auditory bullae slightly less inflated and with external auditory meatus slightly smaller.

From *Peromyscus truei gilberti*, known to us by topotypes and abundant material from other parts of its range, *nevadensis* differs as follows: Tail shorter and body longer; length of tail averages 86 as opposed to 101 per cent of length of head and body; color paler, resulting from a reduction in tone of cinnamon and also a lesser amount of blackish in the upper parts; skull averages larger in every measurement taken except length of palatine foramina and least interorbital constriction; rostrum relatively as well as actually longer; auditory bullae slightly more inflated, and external auditory meatus considerably larger.

Judging from Bailey's (No. Am. Fauna, no. 55, p. 188, 1936) description of *Peromyscus truei preblei*, *nevadensis* is larger, has a tail relatively shorter (86 as opposed to 94 per cent of length of head and body), and the skull has a much longer rostrum.

*Remarks*.—The range of this long-bodied, light-colored pinyon mouse probably does not meet the range of *preblei*, and is separated from that of *gilberti* by the range of the race *truei*, which extends northward at least to near 41°

north latitude in the low western part of Nevada. Intergradation with *P. t. truei* is indicated by a specimen from Greenmonster Canyon, 7500 feet altitude, Monitor Range, Nye County, Nevada, which has a relatively long body suggestive of *nevadensis*, a color intermediate between that of *truei* and *nevadensis*, though nearer the latter, and a skull which is small as in *truei*, to which race it is referred. Specimens from southern White Pine County, Ne-

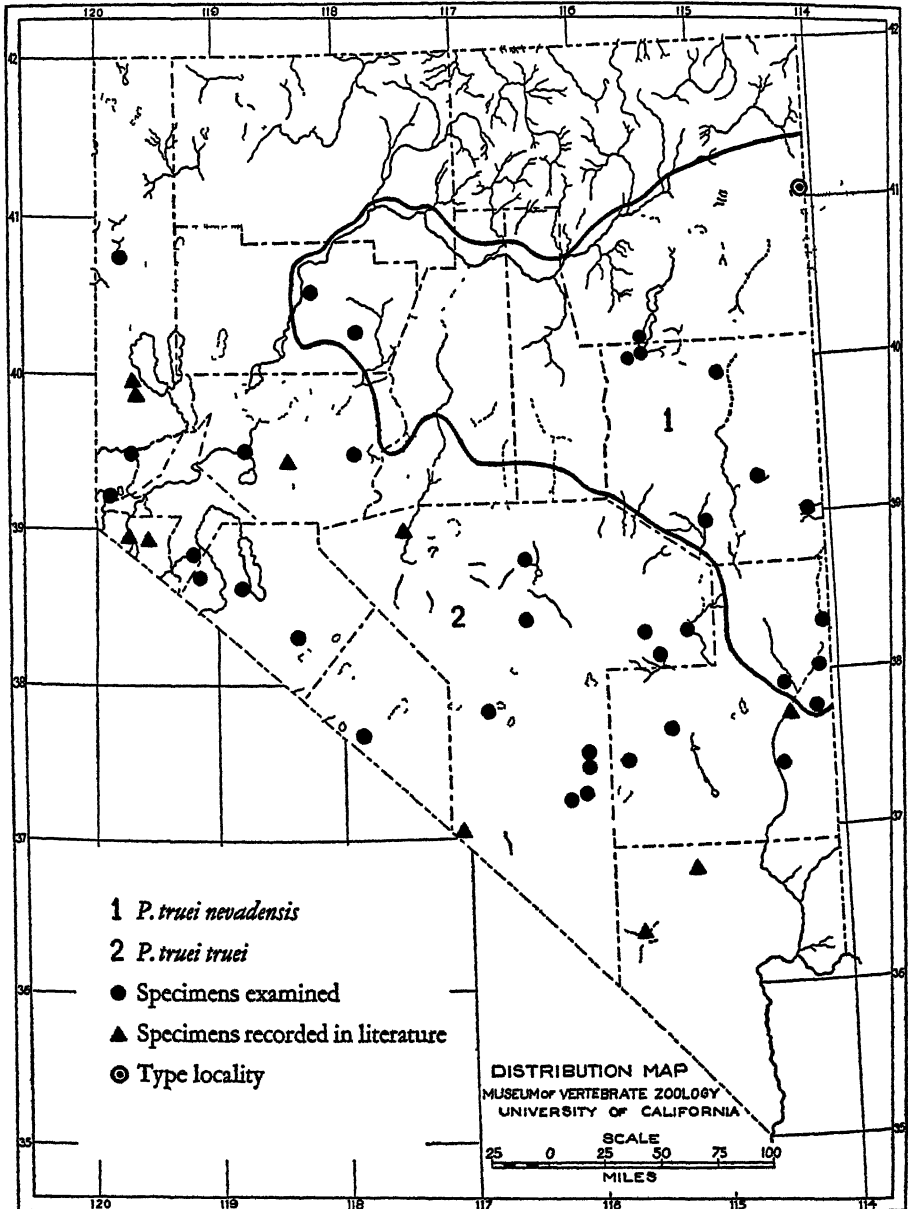


Fig. 1. Map showing the known occurrence of two subspecies of the pinyon mouse, *Peromyscus truei*, in Nevada.

vada, referred to *nevadensis*, are variously intermediate toward *truei*: from Cleve Creek, the two specimens seen are more like *truei*; three from Lehman Cave are light colored and have uninflated bullae like *nevadensis*, but the size of skull and body is as in *truei* in one of the two adults, and as in *nevadensis* in the other adult; five adults from Water Canyon are intermediate in body proportions but are nearer *truei*, the color is definitely nearer that of *truei*, and the cranial characters as a whole are almost exactly intermediate, though possibly a trifle nearer *nevadensis*. Specimens from still farther south, at a point  $3\frac{1}{2}$  miles north of Ursine, are referable to *nevadensis* but at the same time show approach to *truei* in having relatively long tails. Otherwise, specimens from northeastern Lincoln County agree well with *nevadensis*, except that the two adults from 11 miles east of Panaca have skulls intermediate in size between those of *nevadensis* and *truei*. These resemblances to *truei* in specimens from southern White Pine and eastern Lincoln counties, we think, reflect the influence of the *truei* stock to the eastward in Utah as well as that of the *truei* stock immediately to the southward. All the Nevadan specimens just mentioned are referred to *nevadensis*, even the series from Water Canyon in which the sum total of characteristics is more as in *truei*, because the average of all the specimens from that general region is nearer that of *nevadensis*.

When Osgood (No. Am. Fauna, no. 28, 1909) revised this species, he had at most two specimens from the geographic area of occurrence which we have assigned to *nevadensis*. One of his specimens is recorded as from Panaca, which is at the southernmost boundary of the range of *nevadensis*. The other specimen is listed as from the "Reese River" and might or might not fall within the range here ascribed to *nevadensis*. On our distribution map we have shown it as within the range of *P. t. truei*. We have not examined these two specimens.

*Specimens examined*.—Total number, 58, all from Nevada and, unless otherwise indicated, in the Museum of Vertebrate Zoology: *Pershing County*: El Dorado Canyon, 6000 ft., Humboldt Range, 1; S slope Granite Peak, East Range, 2. *Elko County*: Pilot Peak,  $\frac{1}{2}$  mi. W Debbs Creek, 6000 ft., 18; W side Ruby Lake, 3 mi. N White Pine County line, 6700 ft., 1 (coll. Ralph Ellis). *White Pine County*: W side Ruby Lake, 3 mi. S Elko County line, 7000 ft., 5 (coll. R. Ellis); Overland Pass, E slope Ruby Mts., 8 mi. S Elko County line, 1 (coll. R. Ellis); Cherry Creek, 6800 to 6900 ft., 6; Cleve Creek, 6900 ft., Shell Creek Range, 3; Lehman Cave, 7400 ft., 1;  $\frac{1}{2}$  mi. W Lehman Cave, 7500 ft., 2; Water Cañon, 8 mi. N Lund, 11. *Lincoln County*: Lat.  $38^{\circ} 17' N$ ,  $\frac{1}{4}$  mi. W Utah-Nevada Boundary, 7300 ft., 1; Eagle Valley, 5600 ft.,  $3\frac{1}{2}$  mi. N Ursine, 2; 11 mi. E Panaca, 6500 to 6600 ft., 4.

#### *Peromyscus truei truei* (Shufeldt)

1885. *Hesperomys truei* Shufeldt, Proc. U. S. Nat. Mus., 8:407, September 14, 1885. Type from Fort Wingate, McKinley County, New Mexico.

*Range*.—In Nevada, southern and western parts of the state (see map, fig. 1).

*Records of occurrence*.—*Specimens examined*: Total number, 85, from Nevada and, unless otherwise indicated, in the Museum of Vertebrate Zoology: *Washoe County*: 17 mi. W Deephole, 4800 ft., 1; 3 mi. E Reno, 1; 3 mi. SE Incline, 6250 ft., 1. *Lyon County*: West Walker River, 12 mi. S Yerington, 4600 ft., 4. *Churchill County*: Fallon, 4000 ft., 1 (coll. J. R. Alcorn, Fallon, Nev.); Cherry Creek (Spring), 5000 ft., 3. *Mineral County*: 2 to  $3\frac{1}{2}$  mi. SW Pine Grove, 7250 to 7800 ft., 20; Cottonwood Creek, Mount Grant, 7400 to 7900 ft., 4;

TABLE 1  
MEASUREMENTS, IN MILLIMETERS, OF ADULT SPECIMENS OF TWO SUBSPECIES OF PEROMYSCUS TRUEI FROM NEVADA

| M. V. Z.<br>Catalog no.            | Sex | Locality                       | Total length | Length of tail | Length of head<br>and body | Length of<br>hind foot | Greatest length<br>of skull | Basilar length | Greatest<br>breadth of<br>brain case | Interorbital<br>constriction | Length of<br>molars | Shell of<br>bony palate | Palatine slit | Diastema | Postpalatal<br>length | Alveolar<br>length of<br>maxillary<br>tooth row |
|------------------------------------|-----|--------------------------------|--------------|----------------|----------------------------|------------------------|-----------------------------|----------------|--------------------------------------|------------------------------|---------------------|-------------------------|---------------|----------|-----------------------|-------------------------------------------------|
| <i>Peromyscus truei nevadensis</i> |     |                                |              |                |                            |                        |                             |                |                                      |                              |                     |                         |               |          |                       |                                                 |
| 68472                              | ♂   | Pilot Peak, Elko Co.....       | 200          | 94             | 106                        | 23.0                   | 28.9                        | 21.3           | 13.4                                 | 4.6                          | 10.6                | 4.1                     | 5.8           | 7.0      | 10.7                  | 4.2                                             |
| 68476                              | ♂   | Pilot Peak, Elko Co.....       | 202          | 88             | 114                        | 22.0                   | 28.8                        | 21.3           | 13.1                                 | 4.6                          | 10.8                | 4.2                     | 6.0           | 7.1      | 10.4                  | 4.3                                             |
| 46225                              | ♂   | Cherry Cr., White Pine Co..... | 191          | 89             | 102                        | 23.0                   | 28.7                        | 21.0           | 13.4                                 | 4.5                          | 11.0                | 4.5                     | 5.8           | 7.1      | 9.9                   | 4.2                                             |
| 68479                              | ♂   | Pilot Peak, Elko Co.....       | 212          | 97             | 115                        | 24.0                   | 31.1                        | 22.9           | 13.5                                 | 4.5                          | 11.5                | 4.5                     | 6.1           | 7.8      | 11.0                  | 4.4                                             |
| 68480                              | ♂   | Pilot Peak, Elko Co.....       | 201          | 93             | 108                        | 24.0                   | 29.3                        | 21.8           | 13.6                                 | 4.3                          | 10.6                | 4.3                     | 6.0           | 7.2      | 10.6                  | 4.3                                             |
| 6948*                              | ♀   | Ruby Lake, Elko Co.....        | 201          | 96             | 105                        | 23.0                   | 29.1                        | 21.3           | 13.3                                 | 4.7                          | 10.9                | 4.1                     | 6.2           | 7.2      | 10.4                  | 4.3                                             |
|                                    |     | Average of 6.....              | 201          | 93             | 108                        | 23.2                   | 29.3                        | 21.6           | 13.4                                 | 4.5                          | 10.9                | 4.3                     | 6.0           | 7.2      | 10.5                  | 4.3                                             |
| <i>Peromyscus truei truei</i>      |     |                                |              |                |                            |                        |                             |                |                                      |                              |                     |                         |               |          |                       |                                                 |
| 64405                              | ♂   | Pine Grove, Mineral Co.....    | 178          | 87             | 91                         | 23.0                   | 27.9                        | 21.1           | 13.4                                 | 4.5                          | 10.8                | 4.0                     | 6.1           | 7.3      | 9.9                   | 4.3                                             |
| 64410                              | ♂   | Pine Grove, Mineral Co.....    | 187          | 95             | 92                         | 24.0                   | 28.4                        | 21.0           | 13.5                                 | 4.7                          | 10.4                | 4.3                     | 5.8           | 7.2      | 10.0                  | 4.2                                             |
| 64411                              | ♂   | Pine Grove, Mineral Co.....    | 177          | 89             | 88                         | 22.5                   | 28.2                        | 20.4           | 13.0                                 | 4.4                          | 10.7                | 4.2                     | 5.7           | 7.0      | 9.7                   | 4.1                                             |
| 64433                              | ♂   | Mt. Grant, Mineral Co.....     | 191          | 93             | 98                         | 23.5                   | 28.1                        | 21.0           | 12.7                                 | 4.3                          | 10.7                | 4.3                     | 6.0           | 7.3      | 10.0                  | 4.3                                             |
| 64435                              | ♂   | Mt. Grant, Mineral Co.....     | 195          | 98             | 97                         | 24.0                   | 29.1                        | 21.7           | 13.4                                 | 4.5                          | 11.0                | 4.2                     | 6.2           | 7.4      | 10.4                  | 4.3                                             |
| 64418                              | ♀   | Pine Grove, Mineral Co.....    | 183          | 90             | 93                         | 22.0                   | ....                        | 21.0           | 13.3                                 | 4.6                          | ....                | 4.2                     | 5.9           | 7.2      | 10.1                  | 4.1                                             |
|                                    |     | Average of 6.....              | 185          | 92             | 93                         | 23.2                   | 28.3                        | 21.0           | 13.2                                 | 4.5                          | 10.7                | 4.2                     | 6.0           | 7.2      | 10.0                  | 4.2                                             |

\* Collection of Ralph Ellis.

Endowment Mine, Excelsior Mountains, 6500 ft., 2. *Esmeralda County*: 2 mi. S Piper Peak, Silver Peak Range, 7600 ft., 1. *Nye County*: Greenmonster Canyon, Monitor Range, 7500 ft., 1; 8 mi. W Tybo, Hot Creek Range, 6700 ft., 2; Burned Corral Canyon, Quinn Canyon Mts., 6700 ft., 7; White River Valley, 14 to 15 mi. SW Sunnyside, 5500 ft., 2; Garden Valley, 8½ mi. NE Sharp, 8; 1 mi. SW Cactus Spring, Cactus Range, 1; 3 mi. N Indian Spring, Belted Range, 6700 ft., 1; Indian Spring, Belted Range, 7100 ft., 2; ½ mi. NE Oak Spring, 6600 ft., 3; 5 mi. W White Rock Spring, Belted Range, 7300 ft., 6. *Lincoln County*: E slope Irish Mountain, 6900 ft., 11; SW base Groom Baldy, 7200 ft., 2; Meadow Valley Wash, 4000 ft., 5½ mi. N Elgin, 1. D. G. Nichols (MS) records specimens from elevations of 5000 to 6500 ft. in Hardscrabble Canyon, in the Virginia Mountains on the western side of Pyramid Lake, Washoe County. Osgood (No. Am. Fauna, no. 28, p. 169, 1909) records specimens not seen by us from the following places: *Douglas County*: Anderson Ranch; Gardnerville. *Churchill County*: Mountains 16 mi. E Stillwater. Probably *Nye County*: Reese River; Grapevine Mountains. *Lincoln County*: Panaca. *Clark County*: Charleston Mountains. Burt (Trans. San Diego Soc. Nat. Hist., 7(36):417, 1934) also records specimens from Charleston [Mountains] Peak and also in Clark County from the Sheep Range.

*Transmitted March 10, 1939.*





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BY

EMMET T. HOOPER

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# GEOGRAPHIC VARIATION IN BUSHY-TAILED WOOD RATS

BY

EMMET T. HOOPER

(Contribution from the University of California Museum of Vertebrate Zoology)

IN THE twenty-seven years that have elapsed since the appearance of Goldman's "Revision of the wood rats of the genus *Neotoma*" (1910), which forms the starting point for further systematic work with this genus, many specimens of *Neotoma cinerea*, especially from California, Nevada, and Utah, have accumulated in the Museum of Vertebrate Zoölogy. The study of these by William B. Davis and myself was just begun when Davis was called elsewhere; I continued alone the appraisal of the variation displayed by the material.

Certain trends in variation observed in the species include increasing size with increasing latitude. The correlation is thought to be with climatic factors which vary with the latitude. Bushy-tailed wood rats from the northwestern United States, in Montana, Idaho, and Washington, are much larger than those from the southern part of the species' range, in southern Nevada and east-central California. This change in size is a gradual one. Following the same general trend is the amount of difference in size between old adults of the two sexes. Thus, in the north, oldest males are much larger than oldest females; toward the south, this size discrepancy becomes progressively less. For example, the basilar length of the largest male at hand from Pocatello, Idaho, is 9.9 per cent larger than that of the largest female of apparently comparable age from the same place, whereas in two other specimens of comparable age from the southern Sierra Nevada in California, the male is only 4 per cent larger than the female.

Color and degree of pigmentation in this species are apparently correlated with humidity, and perhaps with color of the substratum on which the animals live. Specimens from the southern Sierra Nevada, the southern Great Basin, and the Great Plains side of the Rocky Mountains in Montana are lightest in color tone and are least pigmented; those from the humid belt along the coast of Oregon are darkest in tone and have the greatest amount of pigmentation. The rest of the specimens studied fall within these two extremes of coloration. Those from the northern Great Basin region—in northern Nevada, northeastern California, western Idaho, eastern Oregon, and southeastern Washington—are slightly lighter, in general, than those from the coastal belt of California (and probably southern Oregon), which are, in turn, lighter than the coast-taken specimens from Washington. It should here be pointed out that whitish, light-reflecting, granitic rocks predominate in the southern Sierra Nevada, and probably the southern Great Basin, where the light-colored rats are found. In the northern Great Basin region, an area inhabited by a darker race, dark volcanic flows are extensive. In the coastal region, the relative humidity is much greater in Washington and in the Cascades of Ore-

gon than in northwestern California; in each of these two areas a recognizable race occurs. As stated above, the one at the north is much the darker.

The Columbia River near the seacoast evidently constitutes a barrier to these rats. Specimens from just north of this river have the tail white below and the lighter dorsal color of *occidentalis*, the race occurring in Washington. Those just to the south have a dark undersurface to the tail, a characteristic of the race *fusca*, which ranges southward in the humid coastal belt of Oregon.

Historical factors, or the presence of more arid conditions toward the south, or both, probably account for the limitations of the range of the species in that direction. On higher mountains to the south of the present known range of *N. cinerea*, conditions suitable for its existence apparently are present, but the arid conditions of intervening deserts prevent any nonfortuitous movements to these areas. I find no evidence that the species occurred southward of its present range in the geological past.

Five hundred and one specimens were used in this study. Unless otherwise indicated, specimens are contained in the Museum of Vertebrate Zoölogy. Additional Recent material was made available by H. H. T. Jackson and Remington Kellogg from the collections of the Bureau of Biological Survey and the United States National Museum, by Arthur Svihla from the collections of the State College of Washington, and by Ralph Ellis and H. S. Fitch from their respective private collections. Fossil materials were lent by R. A. Stirton from collections of the University of California Museum of Paleontology. Helpful suggestions and criticisms were offered by (the late) Joseph Grinnell and by E. Raymond Hall. For drafting the map and final typing of the manuscript I am indebted to assistance from the W. P. A. (Official Project No. 465-03-3-192).

Methods and measurements used herein are essentially the same as are described elsewhere (Hooper, 1938:216-217). A detailed description of the skull of *N. cinerea* has been given by Goldman (1910:97).

Description of pelage coloration is given in some detail for *Neotoma cinerea acraia*, page 414. This serves as a basis for comparison of other races, in the accounts of which only the more diagnostic color characters are mentioned. Measurements are in millimeters. Capitalized color terms are used in accordance with Ridgway's Color Standards and Color Nomenclature (1912).

In the succeeding systematic accounts two new subspecies are described. These descriptions are followed by recharacterizations of four previously described subspecies, namely, *Neotoma cinerea cinerea*, *Neotoma cinerea acraia*, *Neotoma cinerea occidentalis*, and *Neotoma cinerea fusca*. This recharacterization has seemed desirable in view of the more complete material now available, which affords a better understanding of the differential characters of those subspecies. Currently recognized subspecies of *Neotoma cinerea* other than the six mentioned above are not here treated in detail; however, they, as well as the six, are listed in a summary, at the end of this report, of the systematic findings of the latest revisers. Topotypes have been examined of all the described forms here arranged as synonyms of these six subspecies, except *N. c. columbiana* Elliot and *N. c. lucida* Goldman; for these two, the conclusion of

the investigator who last critically reported on each is accepted. For disposition of the name *columbiana* see Goldman (1910:101), and of *lucida*, Burt (1934:418-421).

*Neotoma cinerea alticola*, new subspecies

*Type*.—Adult female, skin and skull; no. 11152, Mus. Vert. Zool.; Parker Creek [—Shields Creek, U. S. Forest Service map, edition of 1932]; 5500 feet altitude, Warner Mountains, Modoc County, California; collected June 22, 1916, by N. B. Stern; orig. no. 153.

*Range*.—Mountainous and plateau regions of eastern and northeastern California,

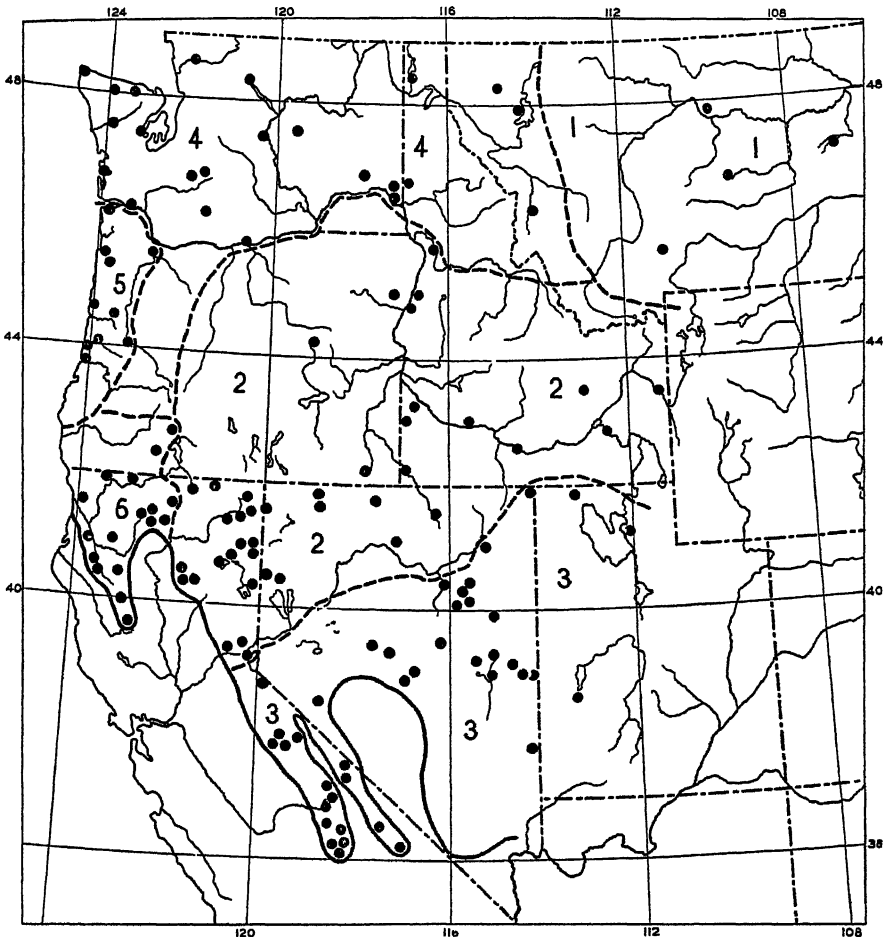


Fig. 1. Map showing ranges of races of *Neotoma cinerea* in the area studied. Dark circles represent localities from which specimens were examined: 1, *Neotoma cinerea cinerea*; 2, *Neotoma cinerea alticola*; 3, *Neotoma cinerea acraea*; 4, *Neotoma cinerea occidentalis*; 5, *Neotoma cinerea fusca*; 6, *Neotoma cinerea pulla*.

northern Nevada, eastern Oregon (east of Cascade Range), and southern Idaho. Known vertical range, from 3900 feet (on Smoke Creek, Washoe County, Nevada) to 8500 feet (at Lake Helen, Shasta County, California).

*Diagnosis*.—Size: large (see table 1); hind foot large; tail relatively short (ratio of tail length to body length averaging less than 79 per cent in every series examined). Color:

similar to that of *pulla* but a lighter brownish cinnamon dorsally. Skull: large and angular; zygomata spread moderately widely; rostrum narrow and deep; bullae large; molar row long; molars massive; sphenopalatine vacuities closed.

*Color*.—Intermediate between that of *pulla* and that of *acraia*; more grayish cinnamon rather than brownish cinnamon as seen in *pulla*, or grayish buff as in *acraia*. Individual hairs of the kinds seen in *acraia*, but with Pinkish Cinnamon instead of Pinkish Buff bands and with black bands more prominent. Tail darker dorsally than in *acraia* and hind feet pigmented as much as 1 cm. distally from tarsal joint.

*Comparisons*.—*N. c. alticola* is distinguishable from *N. c. cinerea* by its darker coloration, larger bullae, and total lack of, or only slightly developed, sphenopalatine vacuities. From *pulla* it differs in its larger size, relatively shorter tail, lighter coloration, more massive skull, larger bullae, longer and more massive molar row, and relatively longer palatal bridge. From *occidentalis*, *alticola* is distinct as follows: color much lighter, hind feet light (dusky area less extensive), tail shorter, bullae larger, molars more massive, and sphenopalatine vacuities narrower. For comparisons with *acraia* see account of that race.

*Remarks*.—*N. c. alticola* is a moderately dark, large race occupying the lava plateau and mountainous areas of the northern Great Basin region. Intergradation with at least three of the six adjoining races is demonstrable. Specimens available from along the southern border of its range show intergradation with *acraia*; for example, a subadult from Tahoe City, California, has the larger size, larger bullae, and darker color of *alticola*, but the smaller and slighter molars of *acraia*. Animals from the Ruby Mountains and Goose Creek, Elko County, Nevada, resemble *acraia* in characters of the pelage, but are like *alticola* in size and in characters of the skull. Specimens from the vicinity of Pocatello, Idaho, are large and have massive molars and closed sphenopalatine vacuities as in *alticola*; but the color is slightly lighter and the bullae comparatively small, characters which may indicate intergradation with *cinerea* or *orolestes*. Specimens from the Lassen Peak region, California, approach *pulla* only in diagnostic characters of the molars. Further account of intergradation with *pulla* and *occidentalis* is given in accounts of those races.

*Specimens examined*.—A total of 141 from the following localities: **Oregon**: *Baker County*: Anthony, 1. *Grant County*: 12 mi. S Canyon City, 5500 ft., 1. *Malheur County*: 21 mi. N McDermitt (Nevada), 5300 ft., 1. **Idaho**: *Idaho County*: John Day Ranch, 10 mi. SW White Bird, 1 (U. S. Nat. Mus.). *Adams County*:  $\frac{1}{2}$  mi. E Black Lake, 6800 ft., 5 (Coll. Ralph Ellis); summit of Smith Mountain, 7500 ft., 2 (Coll. Ralph Ellis); 1 mi. N Bear Ranger Station, SW slope Smith Mountain, 5400 ft., 4 (Coll. Ralph Ellis). *Washington County*: 1 mi. NE Heath, SW slope Cuddy Mountain, 4000 ft., 1 (Coll. Ralph Ellis). *Owyhee County*: 6 mi. W Murphy, 2;  $2\frac{1}{2}$  mi. E Jordan Valley (Oregon), 4500 ft., 1; S Fork Owyhee River, 4500 ft., 12 mi. N Nevada line, 2. *Elmore County*: 3 mi. NE Hammett, 1. *Butte County*: Pioneer, 17 mi. SE Arco, 1. *Twin Falls County*: Shoshone Falls, Snake River, 1. *Bonneville County*: N side South Fork Snake River, 3 mi. W Swan Valley, 2. *Bannock County*: vicinity of Pocatello, 22. **California**: *Siskiyou County*: Indian Well, 4770 ft., Modoc Lava Beds National Monument, 1. *Modoc County*: Steele Meadow, 4700 ft., 1; Sugar Hill, 5000 ft., 7; Joseph Creek, 4800 ft., 1; Dry Creek, 4800 ft., Warner Mountains, 5; Parker Creek [=Shields Creek], 5500 ft., Warner Mountains, 6; 10 mi. SW Alturas, 5000 ft., 1; Duncan Horse Camp, 1. *Lassen County*: 5 mi. N Fredonyer Peak, 5700 ft., 5; Grasshopper Valley, 5400 ft., 1; 4 mi. SW McDonald Peak, 4; 7 mi. N Observation Peak, 5300 ft., 1; 7 mi. E Ravendale, 5000 ft., 2; Spaldings', Eagle Lake, 1; E Lassen City (E of Honey Lake), 2. *Shasta County*: Lake Helen, 8500 ft., 1; Warner Creek, 6600–8300 ft., 6. *Tehama County*: Battle Creek Meadows, 4800 ft., 1; 2 mi. W Black Butte, Lassen Road, 6800 ft., 7. *Plumas County*: Kelley's, 2 mi. N Willow Lake, 5200 ft., 1; Willow Lake, 5600 ft., 1; Hot

Spring Valley, 4. *Nevada County*: Independence Lake, 2. *Placer County*: Cisco, 6000 ft., 4; ½ mi. N Tahoe City, Lake Tahoe, 1. *Nevada*: *Washoe County*: 2 mi. W Vya, 6200–6500 ft., 2; Smoke Creek, 3900 ft., 9 mi. E California state line, 14; Horse Canyon, 5800 ft., Pahrump Peak, 1. *Humboldt County*: Alder Creek, 6000 ft., Pine Forest Mountains, 1; Leonard Creek, 6500 ft., Pine Forest Mountains, 1; 13–14 mi. N Paradise Valley, 6400–6700 ft., 3; 18 mi. NE Iron Point, 4600 ft., 2. *Elko County*: 13 mi. SSW Whiterock, 5600 ft., 2.

*Neotoma cinerea pulla*, new subspecies

*Type*.—Adult female, skin and skull; no. 57077, Mus. Vert. Zool.; Kohnenberger's Ranch, 3200 feet altitude, South Fork Mountain, Trinity County, California; collected June 25, 1932, by C. C. Lamb; orig. no. 16758.

*Range*.—In general, higher regions of Coast and Cascade ranges of northwestern California and southwestern Oregon. From vicinity of Elk Creek, Glenn County, north and east through Trinity Mountains, western Shasta County, southern Cascade Range in eastern Siskiyou County, California, to vicinity of Fort Klamath, Klamath County, Oregon; north and west (from Elk Creek) through South Fork Mountain and Horse Mountain, Humboldt County, to Doctor Rock Peak, Del Norte County, California. Known vertical range from 3000 feet (at Sisson, Siskiyou County) to 9000 feet (on Mount Shasta, Siskiyou County). Zonal range, Transition, Canadian, and locally into Hudsonian.

*Diagnosis*.—Size: small (see table 1); hind foot small; tail long (ratio of tail length to body length averaging over 80 per cent in the series examined). Color: brownish cinnamon dorsally, white or grayish white ventrally; hind feet white above; tail grizzled gray or grayish cinnamon above, white below. Skull: rostrum shallow and relatively long and broad; zygomata spread relatively widely; molar row short and narrow; individual molars less massive than those in any other race studied; auditory bullae moderately large; sphenopalatine vacuities narrow slits (not over 0.2 mm. wide).

*Color*.—As described for *acraia*, except for differences as follows: dorsal coloration brownish cinnamon (individual hairs of the types seen in *acraia* but with Pinkish Cinnamon instead of Pinkish Buff); dusky area of dorsal surface of legs extending distally about 1 cm. from tarsal segments, the rest white or lightly tinged with Pinkish Cinnamon; tail darker dorsally.

*Comparisons*.—*N. c. pulla* is similar in size to *N. c. acraia*, but differs from it in well-marked characters as follows: color darker, tail longer, nasals relatively longer, bullae smaller, molars less massive, molar row shorter. From *fusca*, *pulla* may be distinguished by its smaller size, much lighter color, white ventral surface of tail, light-colored hind feet, less angular skull, relatively longer nasals, and wider spread of zygomata. For comparisons with *occidentalis* and *alticola*, see accounts of those races.

*Remarks*.—*N. c. pulla* is the southwesternmost subspecies of the series of intergrading forms of *Neotoma cinerea*. Of those subspecies occupying the more humid coastal belt, *pulla* is the lightest in color and the smallest in size. It intergrades with *alticola*, *occidentalis*, and probably with *fusca*. Two specimens, one juvenile and one subadult, from Butte Creek, California, approach *alticola* in both skin and cranial characters; adult specimens from here might be more typical of one race or the other. Specimens from Fort Klamath, Oregon, might be placed with either *occidentalis* or *pulla*, but not with *alticola*; here they are included with *pulla*. Two skins only of young individuals from Fish Lake Resort, Jackson County, Oregon, have the relatively long tail characteristic of the coastal races; because of comparatively small size and light color, these animals are referred to *pulla*. I do not know whether the range of *pulla* meets that of *fusca* or of *occidentalis* in the humid belt along the sea coast.



*Teonoma spelaea* Sinclair (1905:148), a fossil species, is based on material obtained from Quaternary deposits in Potter Creek Cave, Shasta County, California. The type specimen consists of the anterior two-thirds of a skull of an animal apparently of subadult age; the teeth are little worn. Some of the characters considered diagnostic of the species by Sinclair seem to me to be well within the range of variation of any subspecies of *N. cinerea* studied. However, the rostrum is broader, shorter, and deeper than that of any skull at hand showing a similar amount of wear of the teeth. The size of this animal must have been greater than that of most Recent animals of comparable age.

In size and characters of the rostrum the type specimen more closely resembles examples of Recent animals from the northern United States, in Montana, Idaho, and Washington, than examples from the vicinity of Potter Creek Cave, California. Even so, the short, broad, deep rostrum is not exactly matched in any other specimen examined. Sixteen skull fragments at hand from another Quaternary deposit, namely, Samwel Cave, Shasta County, can be matched in detail with skulls of *pulla*, the race probably now occurring in the area. If it were known that the geologic age of the two deposits was the same, the type specimen might be considered an extremely large and "abnormal" specimen of *pulla*. With our present knowledge, however, this assumption, cannot be made with safety.

For the time being, then, *Teonoma spelaea* may be treated as a species distinct from other kinds of wood rat. Its closest relationships are with subspecies of *Neotoma cinerea* now occurring to the northward of the type locality of *spelaea*—for example with *N. c. occidentalis*. The differences between *spelaea* and *occidentalis*, however, are apparently no greater than the differences between *occidentalis* and, say, *pulla*. Thus, on the basis of degree of difference, *spelaea* might be treated as a subspecies of *N. cinerea*.

*Specimens examined.*—A total of 69 from the following localities: Oregon: *Jackson County*: Fish Lake Resort, 2 (Coll. H. S. Fitch). *Klamath County*: Fort Klamath, 4 (U. S. Nat. Mus.). California: *Del Norte County*: Doctor Rock Peak, 1. *Siskiyou County*: Poker Flat, 5000 ft., 12 mi. NW Happy Camp, 1; head of Doggett Creek, 5800–6000 ft., 6; vicinity of Weed, 3600–3800 ft., 4; Kangaroo Creek, 2; Jackson Lake, 5900 ft., 6; Sisson, 3000 ft., 1; Castle Lake, 5434 ft., 1; Mt. Shasta, 9000 ft., 1; Butte Creek, T. H. Benton Estate, 2. *Humboldt County*: Horse Mountain, 4700–4900 ft., 6; near Blake Lookout, 5500 ft., South Fork Mountain, 3. *Trinity County*: North Fork of Coffee Creek, 4500 ft., 8; head of Grizzly Creek, 6000 ft., 2; 3 mi. NNW Mad River Bridge, 2900 ft., 1; The Racetrack, 5500 ft., South Fork Mountain, 5; Kohnenberger's Ranch, 3200 ft., South Fork Mountain, 5. *Tehama County*: divide 12 mi. N North Yolla Bolly Mountain, 4400 ft., 1; ½ mi. to 2 mi. S South Yolla Bolly Mountain, 5. *Glenn County*: Elk Creek, 1.

#### *Neotoma cinerea cinerea* (Ord)

*Range.*—Rocky Mountain region in extreme southeastern British Columbia, southern Alberta, and Montana; perhaps in extreme northwestern Wyoming and western South Dakota (see Goldman, 1910:95–98). Vertical range at least from about 3000 feet (near Jordan, Dawson County, Montana) to 5000 feet (at Bozeman, Gallatin County, Montana).

*Diagnosis.*—Size: large (see table 1); tail relatively short. Color: as in *acraia*. Skull: angular; zygomata spreading widely posteriorly; bullae moderate in size; sphenopalatine vacuities open (wider than those in any other race studied—from 0.3 mm. to 0.6 mm. in width).

*Color*.—Indistinguishable, apparently, from that of *N. c. acraia*.

*Comparisons*.—*N. c. cinerea* is compared with *occidentalis*, *fusca*, *acraia*, and *alticola* in the respective accounts of those races. From *pulla*, it differs as follows: size larger, hind foot larger, tail shorter; color lighter and more ochraceous, dorsal sides of hind feet less clouded with dusky or fuscous; skull more angular and massive, nasals relatively shorter, bullae larger, molar row longer, molars more massive, sphenopalatine vacuities larger.

*Remarks*.—Perhaps the range of the subspecies *N. c. cinerea* should be restricted to the region east of the crest of the Rocky Mountains and, in the United States, to Montana. Specimens at hand from central and south-central Montana—at Birch Creek Canyon, Chouteau County, Big Snowy Mountains, Fergus County, and Bozeman, Gallatin County—all have wide sphenopalatine vacuities (in comparison with those of other races studied, but narrower than those in *orolestes*, *rupicola*, and *arizonae*), are light in color (as in *acraia*), and are of large size (as in *occidentalis*). Specimens from the heart of the Rocky Mountains in western Montana, at Upper Stillwater Lake and Flathead Lake, both in Flathead County, are dark colored and have the sphenopalatine vacuities closed or noticeably smaller, as in specimens of *occidentalis* from western Washington.

Probably the exact characteristics (particularly those of the pelage) of adult topotypes of *cinerea* are not known; and specimens in adult pelage from the type locality could not be located. Goldman (*loc. cit.*) had only immature individuals at his disposal. Even the description written by Clark in his journal seems to be based on a specimen in the bluish gray, juvenal pelage, and not on an adult animal (see History of the Expedition, Hosmer, 1902:310). Judging from the topography of the region, it seems to me that specimens from either Birch Creek or the Big Snowy Mountains would show more resemblance to those at Great Falls (the type locality) than would those from either Flathead Lake or Upper Stillwater Lake. I have considered the lighter-colored specimens from the former localities to be typical of *cinerea*.

*Specimens examined*.—A total of 7 from the following localities: **British Columbia:** Kootenay District, Crows Nest Station, 1. **Montana:** *Chouteau County:* Birch Creek, 2 (U. S. Nat. Mus.). *Fergus County:* Big Snowy Mountains, 2 (U. S. Nat. Mus.). *Dawson County:* 7 mi. S Jordan, 1. *Gallatin County:* Bozeman, 1 (U. S. Nat. Mus.).

#### *Neotoma cinerea acraia* (Elliot)

*Range*.—In general, southern Sierra Nevada and southern Great Basin. In California, Sierra Nevada from Monache Meadows and Jackass Meadows, Tulare County, north to vicinity of Woodfords, Alpine County; in White, Inyo, and Panamint mountains and probably in other of the neighboring high desert ranges. In Nevada, Charleston Mountains (*sic* Goldman, 1917:111) north, discontinuously, to the region of Walker Lake, Mineral County, at west, and at east through Ruby Mountain region, Elko County, to extreme northeastern part of the state. In Utah, at least in western part, discontinuously from northern to southern border of state. Perhaps into northern Arizona, at south, and southwestern Wyoming, at north (*cf.* Goldman, 1910:98, under *N. c. cinerea*). Extremes of known vertical range seen in California, from 5000 feet (on Kings River, Fresno County) to 11,000 feet (at Cottonwood Lakes, Inyo County).

*Diagnosis*.—Size: small (see table 1), smallest of the races here considered; tail relatively short (its length averages about 77 per cent of body length in 21 adults from near

Mount Whitney). Color: pale grayish cinnamon-buff dorsally, white or grayish white ventrally; hind feet white above; tail grayish buff above, white below. Skull: lacking massiveness and marked angularity; zygomatic width actually small but relatively large; molars not as massive as in *alticola*, entire row short; sphenopalatine vacuities closed.

*Color*.—Dorsally: Pinkish Cinnamon to Pinkish Buff, although often appearing more grayish because of presence of black tipping of some hairs. Individual coarse hairs Plumbeous at base, subtending, typically, a distal band of black, Pinkish Cinnamon, or Pinkish Buff, but in a few hairs subtending a medial band of Pinkish Cinnamon or Pinkish Buff which in turn underlies an apical black band. Head more grayish (with less of the cinnamon or buffy tint). Laterally: the cinnamon or buffy tints mentioned above more evident on sides and cheeks; dark-tipped hairs fewer. Ventrally: white or grayish white. Individual hairs white throughout, or Plumbeous at base and white terminally—the latter condition most often seen on sides of belly; this leaves the throat, breast, mid-belly, and inguinal regions pure white. Ear: the few hairs present, white. Vibrissae: black, or white, throughout length, or black basally and white distally. Tail: white throughout below; grizzled, Vinaceous Buff to Cinnamon Drab, dorsally; the mass effect here varies, apparently, with the relative number and the degree of wear of the dark and the light hairs. Legs: same as color of dorsal surface but with less black; ankles white, at least ventrally. Front feet: white from tip of toes to wrist; here displaced by the dusky color of the legs or the white of the ankles; ventral surface bare from wrist distally. Hind feet: colored area of body extending distally from tarsal joint on dorsal surface of feet only about 1 cm., rest of surface white; on ventral surface, hairs from heel to region of first plantar tubercle white, rest of distal region naked.

*Comparisons*.—The race *acraia* resembles the race *cinerea* in color, but is distinct from it in the following characters: size smaller, with smaller hind foot; skull less angular and massive, sphenopalatine vacuities closed, or, if open, always much smaller. From *alticola* it differs in smaller size, smaller hind foot, lighter coloration, less angular skull, relatively broader zygomata, smaller bullae, and less massive molars. For comparisons with *pulla* see account of that race.

*Remarks*.—That the bushy-tailed wood rats from the southern Sierra Nevada and southern Great Basin are different from those in Montana was recognized by Elliot (1903b:247–248) and by Goldman (1917:111–112). Elliot described *acraia* from the Sierra Nevada; Goldman named *lucida* from the Charleston Mountains. However, Goldman at an earlier date (1910:98) could find “no characters by which to recognize *T. c. acraia*.” Burt (1934:418–421), in his study of the mammals of the Charleston Mountains region of southern Nevada, compared series from the Charleston Mountains with others from the region of Mount Whitney, California, White Pine County, Nevada, and Fremont County, Idaho. He recognized that the specimens from the south averaged much smaller in size, and he revived Elliot’s name, *acraia*, to apply to these southern extremes of *N. c. cinerea*. Burt also found the differences between topotypes or near topotypes of *acraia* and of *lucida* to be too small to warrant separation of the two. I have studied the comparative measurements given by Burt and find no difference outside the range of variation of *acraia*. Therefore I infer that *lucida* is not a recognizable race. However, I have seen no specimens from the Charleston Mountains and thus can give no first-hand information on the status of *lucida*.

Over the entire range of this geographic race, except in intergrading areas where its range meets that of a darker form, its characteristic light coloration

is constant. However, there is some variation in size and in cranial characters. In Nevada, which is arid, the bullae are larger and the discrepancy in size between old males and old females is more pronounced (particularly in the northern part of the range of the race). Yet, on the whole, the comparatively slight (less massive) molars, not greatly angular skull, closed sphenopalatine vacuities, small size, and light coloration—all characteristic of this race—apply well. Indeed, a large series of specimens from extreme eastern Nevada agrees well in almost every diagnostic character with a series from the region of Mount Whitney, California.

Intergradation of *acraia* with *alticola* occurs where the ranges of the two meet, for example, in the Sierra Nevada of California. Specimens from the vicinity of Woodfords, Alpine County, are slightly darker than examples from any area to the south; however, in cranial characters they agree with *acraia*. One specimen from Tahoe City, Placer County, approaches *alticola* in darker coloration, larger size, and larger bullae, but is nearer to *acraia* in characters of the molars; it is here identified with *alticola*. Specimens from the Ruby Mountains, Nevada, have the light coloration of *acraia* but are closer to *alticola* in size and in several cranial characters; they are included with *acraia*. Four specimens from Utah—Ogden, the Raft River Mountains, and the Beaver Range—all are darker than specimens from Nevada and California; in this character they may grade toward *N. c. orolestes*, a darker race inhabiting more humid country to the east of the range of *acraia*.

*Specimens examined*.—A total of 225 from the following localities: **California:** *Alpine County:* near Woodfords, 5500–5700 ft., 3. *Tuolumne County:* Glen Aulin, 7700 ft., 4; Tuolumne Meadows, 8500 ft., 4; head of Lyell Canyon, 9700–10,800 ft., 6; Ten Lakes, 9200 ft., 1. *Mariposa County:* Cascade Creek, 5900 ft., 1; 1 mi. E Merced Lake, 7500 ft., 3; Vogelsang Lake, 10,300–10,400 ft., 7. *Mono County:* Warren Fork of Leevining Creek, 9200 ft., 1; Williams Butte, 7000 ft., 2; Walker Lake, 8000 ft., 3; near Big Prospector Meadow, White Mountains, 10,300 ft., 5. *Inyo County:* Roberts Ranch, Wyman Creek, White Mountains, 8250 ft., 5; Big Pine Creek, 10 mi. W Big Pine, 8000 ft., 1; Hanaupah Canyon, 8500–9500 ft., Panamint Mountains, 6; 3 mi. E Jackass Springs, 7200 ft., 8; Little Onion Valley, Sierra Nevada, 7500 ft., 11; Onion Valley, 8500 ft., Sierra Nevada, 6; Cottonwood Lakes, 11,000 ft., Sierra Nevada, 16; Little Cottonwood Creek, 9500 ft., Sierra Nevada, 4. *Fresno County:* Bullfrog Lake, 10,600 ft., 5; Kings River, 5000 ft., 4. *Tulare County:* Olancha Peak, 9750 ft., 1; Jordan Hot Springs, 6700 ft., Sierra Nevada, 4; Monache Meadows, 8000 ft., 3; Jackass Meadows, 7750 ft., 8; Twin Lakes, 1. **Nevada:** *Mineral County:* Cottonwood Creek, 7400–7900 ft., Mount Grant, 2; Lapon Canyon, 8900 ft., 2. *Lander County:* Smith's Creek, 6800–7800 ft., 2; Kingston Creek, 7000–7100 ft., 4; Kingston Ranger Station, 7500 ft., 2. *Nye County:* Monitor Valley, 9 mi. E Toquima Peak, 7000 ft., 1; Greenmonster Canyon, 7500–8200 ft., Monitor Range, 2; Toquima Range, 1 mi. E Jefferson, 7600 ft., 1. *Eureka County:* Evans, 1; 8 mi. W Eureka, 1. *Elko County:* Goose Creek, 5000 ft., 2 mi. W Utah line, 6; Steel's Creek, 7000 ft., Ruby Mountains, 1 (Coll. Ralph Ellis); Long Creek, Ruby Mountains, 2 (Coll. Ralph Ellis); Harrison Pass Ranger Station, Green Mountain Canyon, 6050 ft., Ruby Mountains, 3 (Coll. Ralph Ellis); W side Ruby Lake, 3–6 mi. N Elko County line, 6700 ft., 5 (Coll. Ralph Ellis); W side Ruby Valley, 3 mi. N Elko County line, 9 (Coll. Ralph Ellis). *White Pine County:* Willow Creek, 6500 ft., Ruby Mountains, 2 mi. S Elko County line, 3 (Coll. Ralph Ellis); Cherry Creek, 6800 ft., 4; Gleason Creek, 7300 ft., 4; Halstead Creek, 6200 ft., 1 mi. W Illipah, 1; Cleve Creek, 8100–9100 ft., Shell Creek Range, 5; Water Canyon, 8 mi. N Lund, 2; ¾ mi. SE Stella Lake, 10,800 ft., Snake Mountains, 1; Willard Creek, 7700 ft., Spring Valley, 1; mouth of

TABLE 1  
AVERAGE AND EXTREME MEASUREMENTS IN MILLIMETERS AND RATIO IN PERCENTAGES, OF ADULT SPECIMENS OF SIX SUBSPECIES OF NEOTOMA CINEREA

| Total length                                                  | Tail vertebrae | Hind foot  | Length of body | Ratio, tail to body | Basilar length  | Length of nasals | Zygomatic width | Breadth of rostrum | Depth of rostrum | Length of incisive foramen | Length of palatal bridge | Breadth of bulla | Depth of skull | Alveolar length of molars |
|---------------------------------------------------------------|----------------|------------|----------------|---------------------|-----------------|------------------|-----------------|--------------------|------------------|----------------------------|--------------------------|------------------|----------------|---------------------------|
| <i>N. c. cinerea</i> , 1 ♀, Birch Creek, Montana              |                |            |                |                     |                 |                  |                 |                    |                  |                            |                          |                  |                |                           |
| ...                                                           | ...            | ...        | ...            | ...                 | ...             | 20.1             | 27.1            | 8.1                | 8.2              | 12.2                       | 9.5                      | 8.0              | 16.0           | 9.7                       |
| <i>N. c. alticola</i> , 6 ♀♀, Warner Mountains, California    |                |            |                |                     |                 |                  |                 |                    |                  |                            |                          |                  |                |                           |
| 385-368-401                                                   | 169-155-178    | 42-37-45   | 216-211-223    | 78.4-72.8-84.4      | 43.7-44.1-46.1  | 20.2-19.3-21.1   | 26.2-25.8-26.9  | 7.8-7.4-8.0        | 8.1-7.9-8.4      | 11.8-11.0-12.8             | 9.0-8.4-9.4              | 8.6-8.2-8.9      | 17.1-16.6-17.8 | 10.0-9.5-10.5             |
| <i>N. c. acraea</i> , 13 ♀♀, Mount Whitney region, California |                |            |                |                     |                 |                  |                 |                    |                  |                            |                          |                  |                |                           |
| 358-340-381                                                   | 155-137-172    | 39.6-37-42 | 202.7-193-209  | 76.7-67.5-84.6      | 40.95-44.2-39.1 | 18.5-21.7-19.6   | 25.2-25.8-23.9  | 7.5-7.1-8.1        | 7.3-6.9-8.0      | 10.9-9.9-11.9              | 8.9-8.0-10.1             | 7.7-7.3-8.4      | 15.8-15.2-16.3 | 9.4-8.7-9.9               |
| <i>N. c. occidentalis</i> , 1 ♀, western Washington           |                |            |                |                     |                 |                  |                 |                    |                  |                            |                          |                  |                |                           |
| 360                                                           | 155            | 40         | 205            | 75.6                | 40.6            | 18.2             | 24.1            | 7.5                | 7.4              | 11.5                       | 8.4                      | 7.9              | 15.7           | 9.6                       |
| <i>N. c. fusca</i> , 3 ♀♀, western Oregon                     |                |            |                |                     |                 |                  |                 |                    |                  |                            |                          |                  |                |                           |
| 406                                                           | 192            | 47.5-47-48 | 214            | 88.7                | 42.8            | 20.3             | 25.8            | 7.8                | 8.1              | 11.2                       | 9.7                      | 7.5              | 16.4           | 10.1                      |
| ...                                                           | ...            | ...        | ...            | ...                 | 41.9-43.3       | 19.5-20.8        | 25.4-26.4       | 7.7-7.9            | 8.0-8.2          | 10.8-11.5                  | 9.4-10.2                 | 7.4-7.6          | 16.0-16.7      | 9.9-10.3                  |

*N. c. pulla*, 8 ♀ ♀, South Fork Mountain, California

|         |         |       |         |           |           |           |           |         |         |           |         |         |           |         |
|---------|---------|-------|---------|-----------|-----------|-----------|-----------|---------|---------|-----------|---------|---------|-----------|---------|
| 372     | 168     | 39.6  | 204     | 82.9      | 40.7      | 19.4      | 25.5      | 7.6     | 7.6     | 10.8      | 8.8     | 7.3     | 15.8      | 8.9     |
| 342-402 | 130-193 | 34-44 | 193-217 | 60.0-97.0 | 38.1-42.5 | 18.1-20.4 | 24.3-26.6 | 7.1-8.1 | 7.2-7.8 | 10.1-11.8 | 7.7-9.5 | 7.0-7.6 | 15.3-16.3 | 8.4-9.3 |

*N. c. cinerea*, 2 ♂ ♂, Big Snowy Mountains, Montana

|         |         |       |         |           |           |           |           |         |         |           |         |         |           |          |
|---------|---------|-------|---------|-----------|-----------|-----------|-----------|---------|---------|-----------|---------|---------|-----------|----------|
| 387.5   | 162.5   | 43.5  | 225     | 72.3      | 44.4      | 19.5      | 27.5      | 8.25    | 8.05    | 12.35     | 8.8     | 8.25    | 16.85     | 9.95     |
| 385-390 | 155-170 | 43-44 | 220-230 | 67.4-77.2 | 42.5-46.4 | 18.6-20.4 | 25.0-29.4 | 8.2-8.3 | 7.7-8.4 | 12.3-12.4 | 8.5-9.1 | 7.9-8.6 | 16.8-16.9 | 9.9-10.0 |

*N. c. alticola*, 3 ♂ ♂, Warner Mountains, California

|         |         |       |         |           |           |           |           |         |         |           |         |         |           |          |
|---------|---------|-------|---------|-----------|-----------|-----------|-----------|---------|---------|-----------|---------|---------|-----------|----------|
| 396.5   | 162.5   | 43.5  | 234     | 69.45     | 43.8      | 20.0      | 26.4      | 8.0     | 8.3     | 11.8      | 9.0     | 8.2     | 17.1      | 9.9      |
| 385-408 | 158-167 | 42-45 | 227-241 | 69.3-69.6 | 42.5-46.0 | 19.5-20.5 | 24.7-27.3 | 7.8-8.2 | 8.1-8.6 | 11.3-12.5 | 8.5-9.5 | 8.0-8.7 | 16.8-17.7 | 9.6-10.2 |

*N. c. acraia*, 8 ♂ ♂, Mount Whitney region, California

|         |         |       |         |           |           |           |           |         |         |           |         |         |           |          |
|---------|---------|-------|---------|-----------|-----------|-----------|-----------|---------|---------|-----------|---------|---------|-----------|----------|
| 351     | 154     | 42    | 199     | 77.1      | 40.5      | 18.8      | 25.4      | 7.45    | 7.5     | 11.0      | 8.9     | 7.8     | 16.3      | 9.6      |
| 315-379 | 129-166 | 40-44 | 189-214 | 72.5-83.5 | 39.2-42.6 | 17.5-20.5 | 24.4-26.3 | 7.0-7.8 | 7.0-7.9 | 10.4-11.4 | 8.3-9.5 | 7.4-8.1 | 15.3-16.6 | 9.1-10.0 |

*N. c. occidentalis*, 8 ♂ ♂, western Washington

|         |         |       |         |            |           |           |           |         |         |           |          |         |           |         |
|---------|---------|-------|---------|------------|-----------|-----------|-----------|---------|---------|-----------|----------|---------|-----------|---------|
| 412     | 210     | 48.0  | 216     | 91.0       | 46.2      | 20.8      | 27.2      | 7.9     | 8.4     | 12.3      | 9.6      | 7.9     | 16.9      | 9.4     |
| 379-435 | 178-222 | 43-52 | 201-232 | 77.6-104.2 | 42.9-49.3 | 19.1-22.7 | 24.9-29.1 | 7.3-8.3 | 7.7-8.9 | 11.6-13.4 | 9.1-10.3 | 7.5-8.4 | 16.5-17.5 | 8.3-9.9 |

*N. c. fusca*, 9 ♂ ♂, western Oregon

|         |         |       |         |            |           |           |           |         |         |           |          |         |           |          |
|---------|---------|-------|---------|------------|-----------|-----------|-----------|---------|---------|-----------|----------|---------|-----------|----------|
| 421     | 197     | 47    | 224     | 88.8       | 44.7      | 20.5      | 26.9      | 8.2     | 8.4     | 12.1      | 9.8      | 7.9     | 16.9      | 10.0     |
| 400-440 | 165-220 | 44-50 | 202-239 | 69.6-105.0 | 42.8-46.9 | 19.8-21.4 | 26.0-27.8 | 7.8-9.7 | 8.0-9.0 | 11.0-13.4 | 9.1-10.4 | 7.5-8.1 | 16.3-17.2 | 9.4-10.3 |

*N. c. pulla*, 2 ♂ ♂, South Fork Mountain, California

|         |         |       |         |           |           |           |           |         |         |           |         |         |           |         |
|---------|---------|-------|---------|-----------|-----------|-----------|-----------|---------|---------|-----------|---------|---------|-----------|---------|
| 378     | 174     | 44.5  | 204     | 85.45     | 42.05     | 19.8      | 26.25     | 7.75    | 7.75    | 11.8      | 9.0     | 7.1     | 15.9      | 9.2     |
| 375-381 | 172-176 | 43-46 | 203-205 | 84.9-86.0 | 41.8-42.3 | 19.5-20.1 | 26.2-28.3 | 7.7-7.8 | 7.7-7.8 | 11.7-11.9 | 8.9-9.1 | 6.9-7.3 | 15.6-16.2 | 8.9-9.5 |

Pole Canyon, S side Baker Creek, 7300–7500 ft., Snake Mountains, 8; Baker Creek, 7200–8500 ft., 24. *Lincoln County*: 11 mi. E Panaca, 6700 ft., 1. *Utah*: *Box Elder County*: Pine Canyon, 6600 ft., 17 mi. NW Kelton, Raft River Mountains, 2. *Weber County*: Ogden, 1. *Beaver County*: Britts Meadows, Beaver Range, 8500 ft., 2.

#### *Neotoma cinerea occidentalis* Baird

*Range*.—In general, extreme northwestern United States (in Washington, northern Idaho, and western Montana) and southern British Columbia. Known range in area studied: Washington (except, possibly, for area south of Snake River) eastward through Rocky Mountains of northern Idaho and western Montana to vicinity of Hamilton, Ravalli County, and Flathead Lake, Flathead County, Montana. Known vertical range, from near sea level (at Neah Bay, Clallam County, Washington) to 5500 feet (on Mount Adams, Yakima County, Washington).

*Diagnosis*.—Size: large (see table 1); hind foot large; tail long (ratio of tail to body averages 87 per cent in 8 males from western Washington). Color: blackish brown above, white or grayish white below; ankles of forefeet white (at least on sides); hind feet fuscous for about 2 cm. distally from tarsal joint; tail dark reddish brown above, white below. Skull: long, narrow, and angular; bullae small; molar row actually and relatively short; sphenopalatine vacuities narrow (about 0.2 mm. wide).

*Color*.—Dorsally: blackish brown in mass coloration (individual hairs of the pattern seen in *acraia*, but subterminal Pinkish Cinnamon bands shorter and terminal black bands longer). Ventral surface: white, clouded on throat, belly, and undersides of legs; in some specimens, lateral shoulder region suffused with Pinkish Cinnamon. Hind feet: dorsal surface clouded distally from tarsal joint for about 2 cm. Tail: dark reddish brown above, white below.

*Comparisons*.—The following differences distinguish *occidentalis* from *cinerea*: much darker coloration, larger fuscous area on hind feet, longer, darker tail, smaller bullae, shorter molar row, longer palatal bridge, and narrower sphenopalatine vacuities. From *pulla*, *occidentalis* is distinct in larger size, darker color, usually fuscous (as contrasted with white) hind feet, relatively shorter nasals, and narrower spread of zygomata. For comparisons with *fusca* and *alticola* see accounts of those races.

*Remarks*.—Specimens from near Skamokawa, Washington, are as deeply pigmented as examples of *fusca* from across the Columbia River in Oregon, but they have the light tail (ventrally) of *occidentalis*. Eastward from the Columbia River and within the range of *occidentalis*, as here defined, specimens are lighter in color and have a relatively shorter tail than do specimens from nearer the seacoast. In these characters they approach *cinerea* and *alticola*. However, because their color is darker than in either of these two races and because the skulls are characteristic of *occidentalis*, these animals are included with that race. Specimens from Whitman County, Washington, and Latah and Adams counties, Idaho, are “intergrades” between *occidentalis* and *alticola*. Specimens from Whitman and Latah counties are more like *occidentalis* in characters of pelage and of sphenopalatine vacuities, and are intermediate between typical examples of the two races in characters of molars and bullae. The specimens from Adams County, for the most part, have sphenopalatine vacuities as seen in *occidentalis*, but have the longer molar row, more massive molars, larger bullae and lighter color of *alticola*; they are here referred to that race. Specimens from extreme northern Idaho and western Montana grade toward *cinerea* in color, but, everything considered, are more like *occidentalis*.

*Specimens examined*.—A total of 43 from the following localities: **Washington: Clallam County:** Neah Bay, 1 (U. S. Nat. Mus.); Olympic Mountains, Soleduc River, 4000 ft., 1 (U. S. Nat. Mus.); Mount Angeles, head of Little River, 5000 ft., 1 (U. S. Nat. Mus.). **Grays Harbor County:** Quinalt Lake, 1 (U. S. Nat. Mus.). **Mason County:** Hoodsport, 1 (U. S. Nat. Mus.). **Skagit County:** Hamilton, 1 (U. S. Nat. Mus.); head of Cascade River, 5500 ft., 1 (U. S. Nat. Mus.). **Chelan County:** Stehekin, 1075 ft., 1 (Charles R. Conner Mus.); Wenatchee, 1 (Charles R. Conner Mus.). **Grant County:** Grand Coulee, 1 (Charles R. Conner Mus.); Grand Coulee, Fresh Lake, 2 (Charles R. Conner Mus.). **Pacific County:** Shoalwater Bay, 1 (U. S. Nat. Mus.). **Wahkiakum County:** 4–8 mi. E Skamokawa, 3. **Pierce County:** Mount Rainier, 3 (U. S. Nat. Mus.); Mount Rae, Ohanapecosh Hot Springs, 2004 ft., 1 (Charles R. Conner Mus.). **Yakima County:** Mount Adams, 5500 ft., 1 (Charles R. Conner Mus.). **Klickitat County:** Columbia River, opposite John Day River, 1 (U. S. Nat. Mus.). **Pend Oreille County:** Gardiners Cave, 1 (Charles R. Conner Mus.). **Whitman County:** Rock Creek, 1 (Charles R. Conner Mus.); Pullman, 1 (Charles R. Conner Mus.); Wawawai, 2 (Charles R. Conner Mus.). **Idaho: Bonner County:** Priest Lake, 5 (U. S. Nat. Mus.). **Latah County:** Cedar Mountain, Washington State College camp, 4000–4500 ft., 4 (Charles R. Conner Mus.). **Montana: Flathead County:** Upper Stillwater Lake, 3500 ft., 3 (U. S. Nat. Mus.); Flathead Lake, 2 (U. S. Nat. Mus.). **Ravalli County:** Gird Creek, 2.

***Neotoma cinerea fusca* True**

*Range*.—Humid coastal belt west of the Cascade Range in Oregon. Known range: coastal region, from the Columbia River south to Gardiner, Douglas County; east at north to Portland, Multnomah County, and at south to Eugene, Lane County. Probably confined to the Transition Life-Zone.

*Diagnosis*.—Size: large (see table 1); hind foot large; tail long (ratio of tail length to body length averages 88 per cent in 9 males examined). Color: blackish brown dorsally, light cinnamon ventrally (at least on breast and sides of belly); ankles dark; hind feet fuscous above (for at least 2 cm. distally from tarsal joint); tail blackish brown dorsally, only slightly lighter below. Skull: large and angular; molar row long; individual molars moderately massive; bullae small; sphenopalatine vacuities thin slits (about 0.2 mm. wide).

*Color*.—Much the same as in *occidentalis* from western Washington, but darker and with differences as follows: black-tipped overhair more predominant dorsally, almost obliterating the shorter Pinkish Cinnamon-tipped underfur; breast, sides of belly, and undersurfaces of legs suffused with Pinkish Cinnamon; forefeet dusky above, sometimes completely to toes, but most often only about 1 cm. below carpal joint; ankles dark, hind feet fuscous to toes or for about 2 cm. below tarsal joint; tail blackish brown above, slightly lighter below along mid-line, and often tinged with Pinkish Cinnamon, but never white.

*Comparisons*.—Closest affinities of *fusca* are with *occidentalis*, from which race *fusca* differs as follows: color darker, belly and shoulders washed with cinnamon (instead of white), lower surface of tail lighter than upper surface but never white. Skulls of the two races are, to me, indistinguishable. From *cinerea*, *fusca* is readily distinguishable on the basis of the following differences: color much darker over all, tail only slightly lighter below (not white) and markedly longer, hind feet clouded with fuscous (not white), bullae smaller, palatal bridge averaging longer, sphenopalatine vacuities narrower. For comparisons with *pulla* and *alticola* see accounts of those races.

*Remarks*.—Though apparently indistinguishable from *N. c. occidentalis* in characters of the skull, in pelage *N. c. fusca* is well differentiated from it as also from all other races studied. It shows the extreme of dark coloration in the species. A dark reddish brown or black pigmentation predominates over the entire pelage; lighter areas are restricted to small areas on the dorsal sides of the feet and on the ventral surface of the body. The amount of pigmentation in specimens apparently decreases as the distance from the humid coastal belt increases. Two specimens from Eugene, in the Willamette Valley, are lighter



dorsally and have a lighter ventral tail surface; in these features they approach *occidentalis* slightly. All specimens examined from the coastal area north of the Columbia River have the tail white below, a characteristic of *occidentalis*. In all adult specimens from south of this river and within the range of *fusca* the tail is never white below. Two juveniles from Beaverton, Oregon,

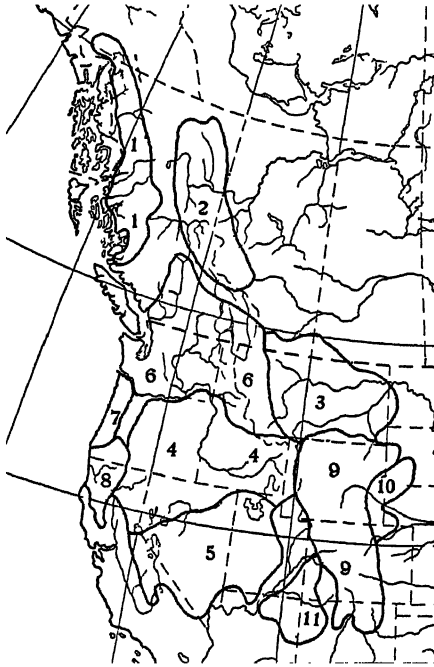


Fig. 2. Map showing distribution of the subspecies of *Neotoma cinerea*. Modified from Goldman (1910:96). Essential changes from Goldman's map involve the states of Washington, Oregon, Idaho, Montana, California, Nevada, and Utah (western part only). The ranges in Canada and the rest of the United States are as given by Goldman.

1, *Neotoma cinerea saramans*; 2, *Neotoma cinerea drummondii*; 3, *Neotoma cinerea cinerea*; 4, *Neotoma cinerea alticola*; 5, *Neotoma cinerea acraea*; 6, *Neotoma cinerea occidentalis*; 7, *Neotoma cinerea fusca*; 8, *Neotoma cinerea pulla*; 9, *Neotoma cinerea orolestes*; 10, *Neotoma cinerea rupicola*; 11, *Neotoma cinerea arizonae*.

have the tail white below, a feature which may be a characteristic of the juvenile pelage. An adult from Portland (a locality north and east of Beaverton and nearer the range of *occidentalis*) is typical of the race *fusca*. No intergradation with *pulla*, the race to the south of the range of *fusca*, is known.

*Specimens examined*.—A total of 16 from the following localities in Oregon: *Clatsop County*: Astoria, 1 (U. S. Nat. Mus.). *Tillamook County*: Tillamook, 1; Blaine, 1. *Multnomah County*: Portland, 1 (U. S. Nat. Mus.). *Washington County*: Beaverton, 2 (U. S. Nat.

Mus.). *Lincoln County*: Yaquina Bay, 1 (U. S. Nat. Mus.). *Benton County*: 5 mi. SW Philomath, 2 (U. S. Nat. Mus.). *Lane County*: Florence, 1 (U. S. Nat. Mus.); Seaton [=Mapleton], 1 (U. S. Nat. Mus.); Mapleton, 1 (U. S. Nat. Mus.); Eugene, 3 (U. S. Nat. Mus.). *Douglas County*: Gardiner, 1.

The races of *Neotoma cinerea*, as understood by the writer, together with the type locality, brief synonymy and range for each, are as follows:

1. *Neotoma cinerea saxamans* Osgood

*Neotoma saxamans* Osgood (1900:33-34)

*Neotoma cinerea saxamans*, Allen (1903:544-546)

*Type locality*.—Bennett City, head of Lake Bennett, Skeena [Cassiar] District, British Columbia.

*Range*.—West of the Rocky Mountains in northern British Columbia; exact limits of range unknown (Goldman, 1910:100).

2. *Neotoma cinerea drummondii* (Richardson)

*Myoxus Drummondii* Richardson (1828:517-518)

*Neotoma Drummondii* Richardson (1829:137-140)

*Neotoma cinerea drummondii*, Merriam (1892:25)

*Type locality*.—Rocky Mountains in latitude 57 degrees; probably near Jasper House, Peace River District, Alberta (*vide* Goldman, 1910:99).

*Range*.—Rocky Mountains of eastern British Columbia and western Alberta, north of the range of *N. c. cinerea* and *N. c. occidentalis* (Goldman, *loc. cit.*).

3. *Neotoma cinerea cinerea* (Ord)

*Mus cinereus* Ord (1815:292)

*Neotoma cinerea*, Baird (1857:499-500)

*Type locality*.—Great Falls, Cascade County, Montana. Name applied by Ord to the ash-colored rat described in the journals of the Lewis and Clark expedition (see Hosmer, 1902:310).

*Range*.—Rocky Mountain region from southeastern British Columbia and southern Alberta south to southern Montana; probably entirely east of the crest of the Rocky Mountains, at least in the United States.

4. *Neotoma cinerea alticola* Hooper

*Neotoma cinerea alticola*, present paper, p. 409

*Type locality*.—Parker Creek [=Shields Creek, on U. S. Forest Service map, edition of 1932], 5500 feet altitude, Warner Mountains, Modoc County, California.

*Range*.—Northern Great Basin area in northern Nevada, northeastern California, southern Idaho, and western Oregon; possibly in extreme southeastern Washington, south of the Snake River.

5. *Neotoma cinerea acraia* (Elliot)

*Neotoma cinerea acraia* Elliot (1903b:247-248)

*Neotoma cinerea lucida* Goldman (1917:111-112). Type from Charleston Peak, Charleston Mountains, Clark County, Nevada

*Neotoma cinerea acraia*, Burt (1934:418-421)

*Type locality*.—Hot Springs, Long Canyon, Mount Whitney, Inyo County, California [=Jordan Hot Springs, near Kern River, Sierra Nevada, Tulare County, California (*vide* Grinnell, 1913:315)].

*Range*.—Southern Sierra Nevada and southern Great Basin regions in California, Nevada, western Utah and northwestern Arizona.

6. *Neotoma cinerea occidentalis* Baird

*Neotoma occidentalis* Baird (1855:335)

*Neotoma cinerea occidentalis*, Allen (1891:287)

*Neotoma cinerea columbiana* Elliot (1899:255). Type from Ducks, Kamloops District, British Columbia

*Type locality*.—Shoalwater Bay, Pacific County, Washington.

*Range*.—Northwestern United States, northern Idaho, Cascade Range of Oregon, western Montana, and Washington; thence north into southern British Columbia.

7. *Neotoma cinerea fusca* True

*Neotoma occidentalis fusca* True (1894:354–355)

[*Neotoma cinerea*] *fusca*, Trouessart (1897:544)

*Neotoma fuscus apicalis* Elliot (1903a:160–161). Type from Gardiner, Douglas County, Oregon

*Type locality*.—Fort Umpqua, Douglas County, Oregon.

*Range*.—Humid coastal belt in Oregon; from Columbia River south to southwestern part of the state.

8. *Neotoma cinerea pulla* Hooper

*Neotoma cinerea pulla*, present paper, p. 411

*Type locality*.—Kohnenberger's Ranch, 3200 feet altitude, South Fork Mountain, Trinity County, California.

*Range*.—Higher regions of Coast and Cascade ranges of northwestern California and southwestern Oregon.

9. *Neotoma cinerea orolestes* Merriam

*Neotoma orolestes* Merriam (1894:128)

*Neotoma grangeri* Allen (1894:324–325). Type from Custer, Custer County, South Dakota

*Neotoma cinnamomea* Allen (1895:331–332). Type from Kinney Ranch, Bitter Creek, Sweetwater County, Wyoming

*Neotoma cinerea orolestes*, Goldman (1910:104–105)

*Type locality*.—Saguache Valley, 20 miles west of Saguache, Saguache County, Colorado.

*Range*.—Rocky Mountain region from northern New Mexico north through Colorado and Wyoming to southern Montana, and thence eastward to the Black Hills, in western South Dakota (Goldman, *op. cit.*:104).

10. *Neotoma cinerea rupicola* Allen

*Neotoma rupicola* Allen (1894:323–324)

*Neotoma cinerea rupicola*, Goldman (1910:107)

*Type locality*.—Corral Draw, southeastern base of Black Hills, South Dakota.

*Range*.—Big Bad Lands region, from southwestern South Dakota through southeastern Wyoming and western Nebraska to northeastern Colorado (Goldman, *op. cit.*:107).

11. *Neotoma cinerea arizonae* Merriam

*Neotoma arizonae* Merriam (1893:110–111)

*Neotoma cinerea arizonae*, Goldman (1910:106)

*Type locality*.—Kear Canyon, Apache County, Arizona.

*Range*.—Northeastern Arizona and southeastern Utah; probably extends northward along the Green River Valley in eastern Utah and through southwestern Colorado and northwestern New Mexico (Goldman, *op. cit.*:106).

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A NEW RACE OF SALAMANDER, *ENSATINA*  
*ESCHSCHOLTZII* *PICTA*, FROM NORTHERN  
CALIFORNIA AND SOUTHERN OREGON

BY  
WALLACE F. WOOD

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# A NEW RACE OF SALAMANDER, *ENSATINA* *ESCHSCHOLTZII* PICTA, FROM NORTHERN CALIFORNIA AND SOUTHERN OREGON

BY

WALLACE F. WOOD

(Contribution from the University of California Museum of Vertebrate Zoology)

IN NOVEMBER, 1933, while collecting amphibians in northern Humboldt and Del Norte counties, California, I obtained a number of salamanders of the genus *Ensatina*. At that time I considered these animals, in spite of their peculiar coloration, to be specimens of *Ensatina eschscholtzii* Gray. As a result of subsequent collecting in northern California, at various seasons during the next three years, and in the winter of 1939, a considerable series of these salamanders was obtained. Careful examination of my own specimens and of pertinent material in the collections of the Museum of Vertebrate Zoology and the California Academy of Sciences showed that, instead of atypical specimens of *Ensatina eschscholtzii*, I really had a hitherto unrecognized subspecies, distinguishable by strongly marked characters showing a high degree of geographical consistency. The new form may be known and described as follows:

## *Ensatina eschscholtzii picta*, new subspecies

*Plethodon eschscholtzii* (part), Grinnell and Camp, Univ. Calif. Publ. Zool., 17, 1917:132; Stejneger and Barbour, Check List, 1917, p. 15.

*Ensatina eschscholtzii* (part), Storer, Univ. Calif. Publ. Zool., 27, 1925:107; Dunn, Anniv. Publ. Smith College, 1926, p. 188; Slevin, Occas. Papers Calif. Acad. Sci., 1928, p. 60; Stejneger and Barbour, Check List, 1923, p. 12, and 1933, p. 13.

*Diagnosis*.—A race of *Ensatina eschscholtzii*, smaller and more delicate than the typical form, from which it is distinguishable by the dark dorsal mottling, a portion of which usually forms on each side, a broken or irregular dorsolateral band, and by the black and yellow mottling of the dorsal surface of the tail.

*Type locality*.—Klamath, Del Norte County, California.

*Range*.—A narrow coastal area, from the vicinity of Weott, Humboldt County, California, northward through Del Norte County at least to Port Orford, Curry County, Oregon. The exact eastern limits are undetermined, but probably lie on the Pacific slope of the outer coast ranges.

*Description of type*.—University of California Museum of Vertebrate Zoology, no. 27471, taken at Klamath, Del Norte County, California, November 4, 1933, by W. F. Wood; adult male; 12 costal grooves; adpressed toes overlap 3 costal interspaces; width of head 20 per cent of length from snout to anterior end of vent; length of head (snout to gular fold) 28 per cent of distance from snout to vent; eye about equal to distance from its anterior corner to tip of snout; snout blunt when viewed from front; profile of upper jaw strongly curved anteriorly; anterior portion of upper lip projecting below lower jaw; angle of jaw directly below posterior corner of eye; a groove from eye to gular fold; limbs long, slender; fingers free, 3, 2, 4, 1 in order of length; toes free, 4, 3, 2, 5, 1 in order of length; vent swollen, papillate; tail measured from anterior end of vent slightly longer than distance from snout

to vent, tail with basal constriction immediately posterior to vent, a series of vertical grooves on sides clear out to tip; tail rugose and glandular on dorsal surface and round in cross section anteriorly, becoming triangular in posterior third; vomerine teeth in two curved series, each extending from a point behind and external to the naris to a point on the median line about opposite the center of the eye; parasphenoid teeth in two patches; a blackish line along groove from eye to gular fold; dorsum light reddish brown; an irregular blackish dorsolateral line from gular fold to posterior end of vent; a line of blackish spots along side from axilla to thigh; this line of spots separated from dorsolateral band by a narrow area of yellowish white and a band of fine brownish flecking; venter yellowish white; tail finely mottled black and yellow dorsally; forearm and thigh with proximal light areas, black flecked and mottled distally; total length, 95 mm.; snout to gular fold, 11.5; gular fold to anterior end of vent, 27; tail, 54.

*Description of female from type locality.*—Museum of Vertebrate Zoölogy, no. 27472; differs from the type as follows: adpressed toes overlap  $1\frac{1}{2}$  interspaces; profile of upper jaw nearly straight; upper lip not projecting below lower jaw anteriorly; vent not swollen, not papillate; a dark line from eye to nostril; dorsolateral band irregular, broken, narrowly margined with light; middorsal line with several blackish spots; an irregular and broken line of dusky flecking from axilla to thigh; total length, 74.5 mm.; snout to gular fold, 11.5; gular fold to vent, 27; tail, 36.

*Variation.*—The general style of coloration is remarkably constant, but, as is to be expected in spotted or blotched patterns, the details are variable. The tail is always mottled, black pigment nearly obscuring the yellow ground color in some specimens, or standing out in bold blotches against an equivalent amount of yellow in others. The dorsal and dorsolateral surfaces may be blotched or mottled with black. In a few animals the black pigment has no regular arrangement, but in most animals the black mottling, or a portion of it, forms an irregular or broken dorsolateral line.

This line may be the only black marking on the dorsum, as it is in the type specimen. There may be a middorsal series of spots or blotches (WFW 34:606, 5 mi. SE Requa). A juvenile (WFW 36:74, 6 mi. E Crescent City) has, on each side, in addition to the dorsolateral band, a continuous narrow black line from axilla to thigh.

Specimens from Castle Rock, Crescent City Harbor, Del Norte County, California (CAS 44872-98), have the markings much reduced, the dorsolateral region being only slightly darkened, with faint blackish blotches posteriorly. The tails are characteristically mottled. Three specimens (CAS 44862-64) from Whale Rock are typical *picta*, and indistinguishable from mainland Del Norte County specimens.

With the exception of the insular series from Castle Rock, the 75 specimens available from Del Norte County are remarkably uniform and show but little significant variation.

*Size.*—*Ensatina eschscholtzii picta* seems to be a smaller and more delicate animal than *E. e. eschscholtzii*. This is illustrated in table 1, based on measurements of specimens in the collection of the Museum of Vertebrate Zoölogy and in my own collection.

*Intergradation and geographical relationships with Ensatina eschscholtzii eschscholtzii.*—Toward the south, *picta* seems to intergrade with *E. e. eschscholtzii* in southern Humboldt County, as it also does to the east, along the

Pacific slope of the outer coast ranges, as near Kneeland and Strong's Station, Humboldt County. Specimens from Carlotta seem referable to *picta*, intergradation presumably taking place between this locality and Strong's Station up the Van Duzen River, at an altitude between 1000 and 2600 feet. Two

TABLE 1  
AVERAGE AND EXTREME MEASUREMENTS, IN MILLIMETERS, OF ADULT SPECIMENS  
OF THE SUBSPECIES OF *ENSATINA ESCHSCHOLTZII*

| Measurement           | <i>eschscholtzii</i><br>Alameda Co. and<br>Contra Costa Co. | <i>eschscholtzii</i><br>Yorkville and Comptche,<br>Mendocino Co. | <i>picta</i><br>Del Norte Co. |
|-----------------------|-------------------------------------------------------------|------------------------------------------------------------------|-------------------------------|
| Number of specimens . | 25                                                          | 25                                                               | 40                            |
| Head and body . .     | 61 2 (52-68)                                                | 53 4 (42-62)                                                     | 44.5 (36-52)                  |
| Total length . . . .  | 113 8 (95-130)                                              | 107 8 (96-119)                                                   | 86 9 (72-104)                 |

specimens (MVZ 14431, 14492) from South Fork Mountain near the Humboldt-Trinity County line are *E. e. eschscholtzii*, and show no approach to *picta*.

In Oregon, intergradation probably takes place just east of a similar narrow coastal strip. A specimen (MVZ 17160) from the Rogue River, 5 miles above Silver Creek, Curry County, is not definitely referable to *picta*. Other specimens which I have examined, from Linn, Jackson, and Tillamook counties, Oregon, seem to be *E. e. eschscholtzii*, although they are rather different from California specimens of that subspecies.

Specimens from points of intergradation are intermediate in coloration, usually having dark unicolor dorsa and mottled tails. In these areas one also finds animals which on an individual basis might be referred to either subspecies.

*Habitat*.—*Ensatina eschscholtzii picta* has been found in all situations where one would expect to encounter a terrestrial salamander. It is especially plentiful in dense redwood forests, but I have taken it in fir and spruce woods and under debris in open areas. Mr. Joseph R. Slevin tells me that he obtained the insular series on Whale and Castle rocks under stones on dry ground.

I wish to thank Mr. Thomas L. Rodgers, of the Museum of Vertebrate Zoölogy, Berkeley, and Mr. Joseph R. Slevin, of the California Academy of Sciences, San Francisco, for assistance and the opportunity to examine material under their care.

*Specimens examined*.—Total number, 96, distributed by localities as follows: **California.** *Humboldt County*: Weott, 6 (WFW 33:1743-47; 39:142); 2 mi. SE Eureka, 1 (MVZ 25745); Carlotta, 9 (MVZ 9148-55, 25727-28); Orick, 2 (CAS 65907-08); *Del Norte County*: Klamath, 30 (WFW 33:1704-13; 33:1715-22; 39:152-63); Requa, 3 (CAS 29097-98, 29100); 5 mi. SE Requa (WFW 34:604-06, 36:59-61); Castle Rock, 27 (CAS 44872-98); Whale Rock, 3 (CAS 44862-64); 6 mi. E Crescent City, 5 (WFW 36:70-74); Smith River, 1 (CAS 29217).

**Oregon.** *Curry County*: Harbor, 1 (CAS 29305); Port Orford, 3 (CAS 29406-08).

*Transmitted by author February 24, 1939.*



